



Dynamic redox conditions control late Ediacaran metazoan ecosystems in the Nama Group, Namibia

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ABSTRACT

The first appearance of skeletal metazoans in the late Ediacaran (~550 million years ago; Ma) has been linked to the widespread development of oxygenated oceanic conditions, but a precise spatial and temporal reconstruction of their evolution has not been resolved. Here we consider the evolution of ocean chemistry from ~550 to ~541 Ma across shelf-to-basin transects in the Zaris and Witputs Sub-Basins of the Nama Group, Namibia. New carbon isotope data capture the final stages of the Shuram/Wonoka deep negative C-isotope excursion, and these are complemented with a reconstruction of water column redox dynamics utilising Fe–S–C systematics and the distribution of skeletal and soft-bodied metazoans. Combined, these inter-basinal datasets provide insight into the potential role of ocean redox chemistry during this pivotal interval of major biological innovation.

The strongly negative $\delta^{13}\text{C}$ values in the lower parts of the sections reflect both a secular, global change in the C-isotopic composition of Ediacaran seawater, as well as the influence of 'local' basinal effects as shown by the most negative $\delta^{13}\text{C}$ values occurring in the transition from distal to proximal ramp settings. Critical, though, is that the transition to positive $\delta^{13}\text{C}$ values postdates the appearance of calcified metazoans, indicating that the onset of biomineralization did not occur under post-excursion conditions.

Significantly, we find that anoxic and ferruginous deeper water column conditions were prevalent during and after the transition to positive $\delta^{13}\text{C}$ that marks the end of the Shuram/Wonoka excursion. Thus, if the C isotope trend reflects the transition to global-scale oxygenation in the aftermath of the oxidation of a large-scale, isotopically light organic carbon pool, it was not sufficient to fully oxygenate the deep ocean.

Both sub-basins reveal highly dynamic redox structures, where shallow, inner ramp settings experienced transient oxygenation. Anoxic conditions were caused either by episodic upwelling of deeper anoxic waters or higher rates of productivity. These settings supported short-lived and monospecific skeletal metazoan communities. By contrast, microbial (thrombolite) reefs, found in deeper inner- and mid-ramp settings, supported more biodiverse communities with complex ecologies and large skeletal metazoans. These long-lived reef communities, as well as Ediacaran soft-bodied biotas, are found particularly within transgressive systems, where oxygenation was persistent. We suggest that a mid-ramp position enabled physical ventilation mechanisms for shallow water column oxygenation to operate during flooding and transgressive sea-level rise. Our data support a prominent role for oxygen, and for stable oxygenated conditions in particular, in controlling both the distribution and ecology of Ediacaran skeletal metazoan communities.

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1. Introduction

The Ediacaran (635–541 Ma) witnessed a profound biological shift from a world with minimal multicellular diversity and evolutionary stasis, to one of new body plans, skeletal types and novel ecologies, culminating in the appearance of modern-style communities by the early Cambrian (Butterfield, 2007; Erwin et al., 2011). Complex, multicellular, body fossils appeared about 575 million years ago (Ma), represented by the soft-bodied Ediacaran biota found initially in deep waters and later in shallow-marine settings (Martin et al., 2000; Narbonne and Gehling, 2003). Embryos of possible metazoans are known from at least ~600–580 Ma (Xiao et al., 1998), while the first unequivocal calcified metazoans were present by ~550 Ma (Germs, 1972). The subsequent rapid diversification of metazoans with hard parts around the Precambrian–Cambrian boundary (541 Ma) marks a step change in biodiversity, the complexity of marine ecosystems, and in the workings of the global carbon cycle. Metazoans demand oxygen to support aerobic metabolisms and skeletal hard-parts, and so it has been presumed that a rise in oxygen, perhaps incrementally, facilitated the evolution of this complexity (Fike et al., 2006; Canfield et al., 2007, 2008; McFadden et al., 2008; Scott et al., 2008).

Chemical tracers reveal a profound change in major biogeochemical cycles during the Ediacaran, such as the global Shuram/Wonoka deep negative C-isotope excursion (Burns and Matter, 1993). This has variously been interpreted as being due to oxidation of a substantial reservoir of organic carbon dissolved in the deep ocean (Rothman et al., 2003; Fike et al., 2006), to a large flux of methane released from clathrates (Bjerrum and Canfield, 2011), or to diagenetic phenomena (Derry, 2010). The models of Bristow and Kennedy (2008), however, suggest that there were not enough oxidants available for the model proposed by Fike et al. (2006), and thus that the Shuram could not have represented a large scale oxidation event. Indeed, the global response of ocean redox chemistry to rising oxygen levels through this period has been shown to be complex (Fike et al., 2006; Canfield et al., 2008; Johnston et al., 2010, 2012b, 2013; Sperling et al., 2013a), including in South China the presence of metastable zones of euxinic (anoxic and sulfidic) waters impinging on the continental shelf and sandwiched within ferruginous [Fe(II)-enriched] deep waters (Li et al., 2010). Detailed reconstructions of ocean chemistry suggest that a globally anoxic and ferruginous deep ocean state existed until at least ~580 Ma, and beyond in certain areas (Canfield et al., 2008; Planavsky et al., 2011; Poulton and Canfield, 2011), whereas surface-water oxygenation is thought to be a near-continuous feature throughout the latter half of the Ediacaran (Canfield et al., 2008). Indeed some have argued that pervasive and persistent oxygenation of the deep ocean did not occur until the later Palaeozoic (e.g. Canfield et al., 2008). There is also evidence to suggest that mid-depth euxinia (free-sulphide in the water column) may have been a feature (but possibly temporally restricted) along some continental shelves at certain times in the Neoproterozoic, but these conditions were sparse compared to the preceding Mesoproterozoic (Canfield et al., 2008; Johnston et al., 2010; Li et al., 2010; Sperling et al., 2013a). The evolution of large metazoans and skeletal hardparts during the Ediacaran period was therefore set within the framework of major perturbations to the C, Fe and S cycles (Des Marais et al., 1992; Logan et al., 1995; Rothman et al., 2003; Fike et al., 2006; Canfield et al., 2007) which are all potentially linked to rising oxygen.

Oxygen requirements in metazoans vary widely, and are determined by size, metabolism, mobility, and the presence or absence of a circulatory system (Vaquer-Sunyer and Duarte, 2008). As a result it has been proposed that metazoans may have been limited to small size (<3 mm), thin body plans, and low diversity communities with simple foodwebs by the relatively low levels of oxygen of the

Proterozoic, with the explosion of larger and ecologically diverse organisms in the late Ediacaran and Cambrian related, in part, to increasing oxygen levels (e.g. Cloud, 1968; Runnegar, 1982). Experimental work has also shown that the oxygen levels necessary to support small, primitive metazoans such as sponges (Porifera) are far lower (Mills et al., 2014) than those required for large, active, and ecologically important animals such as carnivorous predators (Sperling et al., 2013b; Knoll and Sperling, 2014).

In modern marine environments benthic diversity and biomass decreases with bottom-water oxygen levels, as does individual size and abundance until the skeletal macrobenthos is excluded (e.g. Rhoads and Morse, 1971). Hypoxia is a major factor in structuring benthic communities: pelagic-benthic coupling is reduced as are other measures of ecological complexity such as community succession. As oxygen levels decrease, large individuals and long-lived equilibrium species are eliminated, and populations shift towards younger individuals, and smaller and short-lived species that possess opportunistic life histories (Diaz and Rosenberg, 1995). The loss of skeletal biota occurs when oxygen drops below ~0.10 present atmospheric levels, a threshold therefore postulated to fuel the Cambrian radiation (Rhoads and Morse, 1971). In addition, fluctuating and unpredictable redox conditions are deleterious to some metazoans, so establishing stable oxygenated conditions (Johnston et al., 2012), even if pO₂ remained relatively low, may have been just as important as a rise in absolute pO₂.

Some suggest, however, that the Ediacaran oxygen transition was a consequence, not a cause, of metazoan diversification, as the pumping activity of poriferans and cnidarians could have augmented the removal of DOC and smaller phytoplankton from the water column, so substantially enhancing its oxygenation (Butterfield, 2009; Lenton et al., 2014). The evolution of Eumetazoa would have shifted oxygen demand to shelf sea sediments and deeper waters, in turn reducing total phosphorus recycling from sediments so reinforcing through positive feedback the shift to a more oxygenated ocean state (Lenton et al., 2014). These authors argue that this could have facilitated the rise of more mobile and predatory animals.

Such unresolved controversies persist as to the precise role of oxygen in driving metazoan evolution because current records of this interval are limited both spatially and temporally, and without such, a detailed causal understanding of the relationships between anoxia, evolution and carbon cycle processes is not possible.

We focus on the first appearance of calcified metazoans and their ecology, as found in the ~550 to ~541 Ma Nama Group of southern Namibia, one of the best archives of late Ediacaran Earth history (Germs, 1972; Grotzinger and Miller, 2008). Here, soft-bodied Ediacaran biotas and horizontal burrow systems are found preserved in marine siliciclastic rocks, and abundant calcified metazoans occur in shallow to mid-ramp carbonate settings. This distinctive early calcified biota of stem group Eumetazoa, Cnidaria and Bilateria, or Cnidaria (Wood, 2011) terminates globally at the Precambrian/Cambrian boundary at ~541 Ma (Amthor et al., 2003). A greater diversity of body plans and skeletal organisations, including recognisable stem-group members of extant bilaterian phyla, is subsequently recorded in the first 10 Myr of the Cambrian (Knoll, 2003).

To explore relationships between ocean chemistry, the first appearance of calcified metazoans and their ecology, we present new carbon isotope data across two basin transects that capture the final stages of the Shuram/Wonoka deep negative C-isotope excursion (~550 to ~548 Ma). We then consider Fe–S–C systematics and the distribution of skeletal metazoans across these basins to provide detailed insight into the potential role of ocean redox chemistry during this pivotal interval of major biological innovation. We focus on a suite of clastic and carbonate strata which record coeval sedimentation across a mixed clastic-carbonate ramp

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