Title
Rising oxygen concentrations as a driver of macroevolutionary trends in marine communities

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Publication Date
2021

UNIVERSITY OF CALIFORNIA SAN DIEGO

Rising oxygen concentrations as a driver of macroevolutionary trends in marine communities

A dissertation submitted in partial satisfaction of the
requirements for the degree
Doctor of Philosophy

in

Earth Sciences

by

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2021

The Dissertation of Rishi Kumar Sugla is approved, and it is acceptable in quality and form for publication on microfilm and electronically.

University of California San Diego

2021

DEDICATION

To the people and places who, along the way,

became a part of me

and filled this journey

with learning

and love.

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ACKNOWLEDGEMENTS

I would like to thank my committee for their time, energy, and expertise. I'd also like to thank my co-authors and collaborators Dr. Oliver Friedrich, Dr. Jörg Pross, and Dr. Curtis Deutsch for their guidance, availability, and advice on the work presented in this thesis. I'd also like to thank Tom Levy and Jane Willenbring for their time on my committee. Many thanks must also go to everyone in the SIO administration who helped me so much over the years, especially Penny, Gilbert, and Shelley.

Of course, I wouldn't be here without everyone in the Norris Lab. I am grateful to have been in a lab group with such a diverse group of people with so many interests, expertise, and ways of looking at the world. I've learned so much from each and every one of you. Special thanks to Alex, Elizabeth, Rials, Tricia, Wendy, Katie, Jacques, Katrina, Leah, Helen, and many more.

I feel incredibly lucky to have had Dick as my advisor. You've taught me, and all your students, how to approach life as a great adventure. Thank you teaching me so much about the power of reaching outside our disciplines, of letting others grow and explore as they need to, that saying something interesting is sometimes more important (and different) than being "right", that enthusiasm is among the most important trait we can all have, and of sharing ideas openly and often. I would not have finished this dissertation with anyone else as my advisor.

To all the people who have become my family here at San Diego, SIO or otherwise. I am grateful for how you've made San Diego become my home. Despite the pull towards individualism and isolation in academia, you have always reminded me that I have community here. There are too many of you to name here, but I am so grateful to Alyssa, Margot, Garfield, Kasia, Kiefer, Alan, Yury, Catherine, Laura, Ashly, Bridget, Shannon, Daniela, Alfredo, Leticia, Eilene, and Gabo.

To my friends at the Santa Fe Institute who brought me into the world of complex systems and creating a community of friendship and family with me- especially Javier, Laura, Saska, and Jonas. I want to particularly thank Louisa Di Felice for the creativity, perspective, nuance, and kindness she brings with her wherever she goes. Our creative partnerships bring me so much hope, and I'm excited for many more years of us dreaming new possibilities and projects together. To Shaun, Cloet, Manu, and Chiara who I came to know and love at the Urbino Summer School in Paleoclimatology. Thank you for letting me be part of your lives and find a home as my research brought me to Europe.

I am eternally grateful for CIEJ for inviting me to be part of your resistance and struggle. You helped my life feel full, centered, and grounded many times throughout this entire process. Thank you to the communities of Coyo and Salinas Grandes for letting us be in solidarity with your struggle.

To Charlotte Grubb who has somehow become family to me despite our only ever hanging out once in person. Our conversations that cover any and every topic help me feel seen, heard, and understood. The world is unbelievably lucky to have you in it. How you approach struggle, resistance, and revolution is inspiring.

To Lydon Alves who became my brother after we met so randomly in Turkey. Even though there is an ocean between us, I always know it won't be long before life allows us to reconnect. I appreciate how our conversations have expanded my mind.

RJs, life wouldn't be the same without you all. Our annual trips are so important and grounding to me. Your friendship since college has only become more special to me as the years go on and we somehow grow together. Max, Paul, Ross, Kyle, Jordan, and Jon- you all mean so much to me. To Martin, your curiosity, reflectiveness, and kindness are so unique. Our our conversations through my worst moments of the past few years have kept me afloat. I can’t thank you enough. To my dear friend Travis, I’ve appreciated having you in my life since our days in Morocco. Having you in my life to talk about politics, philosophy, and wilderness has been a gift.

To Nicole and the sweetest dog on the planet, Ollie. You are both my rocks, my home, and my heart. I love you both and our adventures together are only beginning. You make the world feel small and expansive at the same time, like everything is within reach. You have, against all odds given the state of the world, made this past year filled with joy. Your kindness and silliness knows no bounds. You continuously surprise me with all the facets of who you are. I love you. To Ollie, thanks for letting me into your very selective pack and showing me how weird, cute, and playful you are.

My family near and far, Indian and Borikén, you all have been incredibly important for this process and shaping who I am. To my tías and tíos, my tau, taiis and bua, my cousins scattered all over the world, I love you and thank you for being part of this. To my baba and ma who are no longer with me. To my abuela who has taught me much about strength, self-reliance, and resilience. A special shout out to my titi Sarah who has fed me multiple times throughout my dissertation and gave me a second home in LA I could always run off to.

To my brilliant sisters Sarika and Monisha. You have taught me so much, through difficult times and good ones, about being fearless. You are both so brave, smart, and talented. You are inspirations to me and I am lucky to be your brother.

To my mom and dad. What is there to say? These past years have made me realize how much of both of you are in me. I am proud to be your son, and to do my best to live up to the values you both taught me. Of course, I would not be here without you both. I love you both.

For this last line I want to thank my grandfather, Arnaldo Muñoz. He was my hero and my inspiration. My summers in Mayagüez with you picking parchas and playing with lagartijos did more to shape who I am than almost anything else I can remember. You taught me to love history, nature, poetry, good food, and compelling stories. I miss you more than I can ever describe, and wish you were here to see the end of this dissertation. I hope this would make you proud.

Chapter two has been submitted for publication and is in review in Science Advances and will appear as: Sugla, R. K., Friedrich, O., Pröss, N. M., Norris, R.D. Secular trends in Phanerozoic carbonate sediment color. Science Advances.(2021). The dissertation author was the primary investigator and author of this paper.

Chapter three has been prepared for submission to the journal Proceedings of the National Academy of Science and may appear as: Sugla, R. K., Norris, R.D. Increased metabolic demand in the Mesozoic Marine Revolution tracks rising oxygen concentrations. Proceedings of the National Academy of Science. (2021). The dissertation author was the primary investigator and author of this paper.

Chapter four has been prepared for submission to the journal Science and may appear as: Sugla, R. K., Deutsch, C.A., and Norris, R.D. Is the modern deep-sea biota an analog for Paleozoic communities? Science. (2021). The dissertation author was the primary investigator and author of this paper.

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ABSTRACT OF THE DISSERTATION

Rising oxygen concentrations as a driver of macroevolutionary trends in marine communities

by

Rishi Kumar Sugla

Doctor of Philosophy in Earth Sciences

University of California San Diego, 2021

Professor Richard D. Norris, Chair

The onset of the Phanerozoic (541 Ma to present) marks a transition point in the evolution of life on Earth. The evolutionary dynamics of this period and its linkages to the physical environment have long been the focus of paleontologists. In this dissertation, I investigate the role of changing oxygen concentrations on the long-term evolutionary trends in Phanerozoic oceans. In particular, I focus on the Mesozoic Marine Revolution, a period of rapid evolutionary transition towards increasingly active communities. In contrast to canonical model reconstructions of atmospheric oxygen during Phanerozoic which show little correlation to evolutionary trends in the marine fossil record, the data presented here suggest an important role for oxygen. I first construct a record of carbonate sediment color to track redox state at the sediment-water interface through time and demonstrate that, despite persistently high levels of atmospheric oxygen, benthic environments may have been poorly oxygenated until 200 million years ago. This record opens up the possibility that shallow marine communities faced selective pressures from oxygen-limited environments until about the time of the Mesozoic Marine Revolution. Building on the sedimentary evidence for a Mesozoic rise in ocean oxygenation, my second chapter builds a quantitative record of metabolic rates in marine communities using modern metabolic rates combined with molecular clock and fossil record ages. This record illustrates that pronounced shifts in metabolic demand occurred during the Mesozoic Marine Revolution from increasing body size and oxygen availability in shallow marine environments. I expand upon this finding by quantifying temperature and oxygen state spaces of living organisms to show that taxa from clades with Paleozoic origins occupy a lower temperature and dissolved oxygen space than clades evolved in the Mesozoic or later. This suggests temperature and oxygen conditions of the deep-sea may act as a barrier against Mesozoic clades and provide refugia for formerly shallow marine Paleozoic communities. In summary, the data presented from this thesis suggest that low oxygen concentrations acted as a limiting variable in the evolution of metabolically active fauna. The data also suggest Paleozoic deep-water communities experienced dissolved oxygen concentrations that varied significantly from equilibrium with the atmosphere.

CHAPTER 1

INTRODUCTION

1. BACKGROUND

The partial pressure of oxygen (pO_2) in the ocean and atmosphere is linked to nutrient regeneration in the water column, energetics of marine communities, metabolic rates of organisms, and organic matter recycling (Boynton & Kemp, 1985; Donald E. Canfield, 1993, 1994; R. J. Diaz & Rosenberg, 2008; Robert J Diaz & Rosenberg, 1995; Ingall & Jahnke, 1994; Rubalcaba, Verberk, Jan Hendriks, et al., 2020). Over multimillion year timescales, the dynamics of oxygen partial pressures in the ocean and atmosphere also affect processes such as weathering, the long-term carbon cycle, redox state in the water and sediment column, and the evolution of life (Fennel et al., 2005; Lenton, 2001; B. Mills et al., 2014; Reinhard et al., 2016). Understanding of how oxygen partial pressures in the ocean and atmosphere affect these long-term processes is limited by the short temporal duration in which modern oceanographic data has been collected. In this thesis, reconstructions of marine and atmospheric oxygen partial pressure and evidence from the geologic and fossil records are used to examine the coupling between oxygen and processes occurring over the past ~500 million years.

The geologic record clearly documents the initial rise and accumulation of atmospheric oxygen in the early Proterozoic (~ 2.5 Ga), a period known as the Great Oxidation Event (GOE) (Buick, 2008). The GOE (2.4-2.3 Ga) is correlated with radiations of cyanobacteria that promoted accumulation of oxygen in the oceans and atmosphere and the destruction of oxygen sinks, such as through the deposition of massive banded iron formations (Anbar et al., 2007; Donald E Canfield et al., 2013; Goldblatt et al., 2006). Following the Great Oxidation Event, geochemical records indicate that oxygen concentrations likely remained between ~<0.001 and 0.1 percent of present atmospheric level (PAL) until an additional rise in atmospheric oxygen in the Neoproterozoic, beginning at ~700 Ma (Och & Shields-Zhou, 2012). The Neoproterozoic rise is linked to the appearance of multicellular eukaryotes and metazoan life and oxygen concentrations that exceed 0.1 PAL for the first time in Earth history (Lenton et al., 2014; Planavsky et al., 2014a).

The record of atmospheric oxygen is not well constrained after the Neoproterozoic rise in atmospheric pO_2. Geochemical models and proxy evidence offer some bounds on Phanerozoic (~544 Ma) O_2, although in practice these offer only general constraints. Many proxy systems track particular thresholds in isotopic and trace element systems that document the passing of particular levels of environmental oxygenation, rather than tracking O_2 over a range of values (Dahl et al., 2010b; Glasspool & Scott, 2010).

Our understanding of O_2 history following the Great Oxygenation Event in the Proterozoic, comes substantially from paleoredox proxies such as mass-independent fractionation of sulfur, Cerium anomalies, and deposition of banded-iron formations, which provide evidence for the Great Oxidation Event major ~2.4 - 2.3 billion years ago (Ga) (Donald E Canfield, 1998; Farquhar, 2000). In the Ediacaran, paleoredox proxies such as the ratio of highly reactive iron to total iron, Uranium isotopes, and enrichment of redox sensitive trace metals such as Molybdenum (Mo), Vanadium (V), Rhenium (Re) and Chromium (Cr) to track changes in oxygenation (Hugh C. Jenkyns, 2010b; Planavsky et al., 2014b; Raiswell & Canfield, 1998; Wilkin et al., 1996). These proxies rely on redox reactions which change oxidative state of trace metals at threshold concentrations of oxygen. Such methods are less suitable at high levels of atmospheric oxygen that persistently exceed the thresholds needed to change oxidative state of trace metals (Buick, 2008). Others, like many marine geochemical proxies, record broad ranges of ocean O_2 levels, but these need not be closely aligned with atmospheric O_2 levels, particularly if the proxy systems record pore water O_2 in sediments (Dahl et al., 2010a, 2014; W. Lu et al., 2018; Z. Lu et al., 2010, 2016). This dissertation contributes to our understanding of Phanerozoic oxygenation by using proxies based on the redox state of carbonate sediments and the physiological activity of organisms.

The Phanerozoic (541Ma- Present) atmosphere was persistently oxygenated at levels sufficient to support metazoans with body plans similar to modern organisms (R. a. Berner et al., 2005; Saltzman, 2005). Models of Phanerozoic oxygenation are typically based on isotopic data, proxy evidence, or a combination of both (Arvidson, 2006; Robert A. Berner, 2006; Van De Velde et al., 2018). Some of the earliest estimates of changing atmospheric oxygen throughout the Phanerozoic were based on isotopic mass balance coupled to models of the carbon and sulfur cycle. These canonical models have suggested that atmospheric oxygen rose to near modern levels by the early Paleozoic (54 to 251.02 Ma), with an absolute high in atmospheric oxygen in the Carboniferous (358.9 - 298.9 Ma) (Royer et al., 2014). Carbon cycle models commonly suggest that pO2 may have exceeded the modern value in the Carboniferous--- a byproduct of extensive coal deposition in wetland ecosystems suggested to be caused by a lack of lignin-consuming organisms or, more recently, a byproduct of Carboniferous climate and tectonic arrangements (Belcher et al., 2010; R. A. Berner, 2009; Holland, 2006). In recent years, there has been an increase in both complexity and diversity of proxies used to reconstruct atmospheric oxygen, yet all show a wide range of estimated atmospheric oxygen concentrations at any given time during the Phanerozoic (Krause et al., 2018; Mills et al., 2016). Proxies such as charcoal abundance in the geologic record have been used to bound minima and maxima of atmospheric oxygen, and offer perhaps one of the tightest constraints on ancient pO2--suggesting that atmospheric oxygen reached levels sufficient to support ignition (~17% PAL) by the Late Silurian (427.4 – 419.2 Ma) (Belcher & McElwain, 2008; Scott & Glasspool, 2006). Outside of these general constraints--- a peak in Carboniferous atmospheric pO2 and reaching ~17% PAL in the Late Silurian, little agreement exists between models (Mills et al., 2016).

Both proxy records and carbon cycle models have been utilized to examine feedbacks between oxygenation and biological evolution. Paleozoic gigantism of terrestrial arthropods, for example, has been linked to the rise in atmospheric oxygen spurred by coal deposition in the Carboniferous (Harrison et al., 2010; Vermeij, 2016). Similarly, modelled increases in atmospheric oxygen over the past ~205 Ma have been linked to radiations of placental mammals (Falkowski, 2005). A potential issue with such models and observations is that atmospheric oxygen concentrations are generally assumed to reflect concentrations of dissolved oxygen in marine environments. In modern oceans oxygen concentration often deviates from equilibrium with the atmosphere with depth, temperature, and primary production. Indeed, pronounced trends and major evolutionary events recorded in the marine geologic record show little correlation with model estimates of atmospheric oxygen (Keeling et al., 2010). This apparent contradiction between pO_2 models and the marine fossil record suggests a need to establish tighter constraints on ocean oxygen concentrations during the Phanerozoic in order to assess potential links to the evolution of life in marine environments.

2. RESEARCH SIGNIFICANCE

This dissertation expands understanding of the complex linkages between oxygen concentrations in the ocean and the evolution of marine ecosystems by quantifying and comparing fundamental, first-order patterns in the geologic and fossil records. The data collected focuses on macroevolutionary trends across the Phanerozoic (541 Ma -- Present), the age of visible of life on Earth. In particular, I develop a novel proxy for marine oxygen concentrations to assess the role that changing dissolved oxygen concentrations may have played as a driver of the Mesozoic

Marine Revolution (MMR). The MMR was a period of a rapid evolutionary change that began in the Early Jurassic characterized by increases in motile fauna and rates of burrowing, the diversification of novel predation strategies (and defensive strategies against such predation), and an overall rise in complexity of ecosystems (Allmon & Martin, 2014a; Buatois et al., 2016a; Finnegan, 2013; Oji et al., 2003). The data presented here alters our understanding of oxygen and evolution over the past 541 million years. This thesis provides evidence in the form of sedimentary records, metabolic data, and through quantification of temperature and oxygen state space of living organisms representative of Paleozoic and Mesozoic clades to show that ecophysiological constraints provide broad explanatory power for major trends in the evolution of life in marine environments. These findings in particular contribute to the scientific understanding the physiological constraints on the evolution of shallow marine communities during the Phanerozoic, and provide evidence that oxygen concentrations at the sediment-water interface were distinctly different from the atmosphere. We show that low oxygen concentrations were likely a limiting variable acting against metabolically active organisms prior to the MMR and highlight the physiological mechanisms behind the similarities between Paleozoic shallow marine taxa and those in modern-deep sea communities.

3. OUTLINE OF THE DISSERTATION

In Chapter 2 I develop a novel proxy for oxidation state at the sediment-water interface using the reflectance of carbonate sediments. Sediment color tracks redox state of benthic environments and can be used as a qualitative proxy for oxygen and organic matter abundance at the time of deposition. I introduce the mechanics behind this proxy and construct a record of Phanerozoic carbonate sediment from geologic sections worldwide. This record tracks secular changes in the oxygenation state of carbonate sediments through time. I find that Paleozoic carbonates are nearly exclusively colored shades of grey. Sediment color is broadly governed by the availability of organic matter and the formation of reduced minerals in pore waters such as pyrite (Giosan et al., 2002; Myrow, 2003). Hence, grey sediments track low pore water oxygenation, a condition attributed to the burial of organic matter in greater abundance than can be respired by oxygen during aerobic respiration. I infer that Paleozoic sediments were deposited under sufficiently low O_2 bottom waters that the pore waters were frequently driven into anaerobic metabolic processes in sediments. The temporal evolution of sediment color implies that carbonate sediments for much of the Paleozoic and early Mesozoic were driven into a reduced state where O_2 was completely consumed and anaerobic metabolisms took over, producing sedimentary pyrite. Notably, starting in the Early Jurassic (~200 Ma), I observe an abrupt shift in the abundance of well-oxygenated carbonate sediments across nearly all depositional environments from shallow marine reefs to deep sea mud. By ~100 Ma, nearly all carbonate sedimentary rocks have oxidized colors, an observation I infer to reflect the widespread efficient consumption of organic matter such that sediment microbiota are rarely pushed into anaerobic metabolisms by low pore water O2 concentrations. I also examine how the paleogeography of the fossil record and that most Palaeozoic sediments come from shallow epeiric environments skews our understanding of Phanerozoic Earth system dynamics.

In Chapter 3, I compile a large database of metabolic rates from modern marine organisms normalized to the same units and temperature. This database includes over 20,000 respiration measurements from over 1,000 species. The species are placed on the geologic timescale through molecular clock and paleobiological data used to estimate when clades originated. Under the assumption of phylogenetic conservatism, this dataset suggests that increased community energetics in the Mesozoic and Cenozoic were the result of body size and activity level increases of marine organisms. Additionally, I explore the possibility that low oxygen concentrations may have acted as a selective pressure against larger body sizes in the Palaeozoic and Early Mesozoic.

In Chapter 4, I explore the anecdotal observation that living species typical of the Paleozoic, like stalked crinoids and brachiopods, are common in the depths of the modern ocean. I explore the possibility that deep-sea habitats mimic the physiological conditions under which animals evolved in the Paleozoic, such as low environment pO_2 . In particular, I hypothesize that taxa with Paleozoic origins that evolved in a low O_2 world may be able to outcompete younger clades in modern environments where low pO_2 or low environmental temperatures limit the activity level organisms. I use distributional data from modern marine organisms to quantify the temperature and oxygen state space they inhabit. We quantify differences between these groups by plotting their occurrences in their environmental pO_2/temperature space to show that species belonging to clades with Paleozoic origins consistently occupy habitats with lower pO_2, and lower temperatures than Mesozoic clades. These results provide evidence that low dissolved oxygen concentrations and low temperatures common in the deep-sea may have acted as a selective pressure against the highly active Mesozoic fauna and provided refugia for organisms with originations in the Paleozoic.

CHAPTER 2

SECULAR TRENDS IN PHANEROZOIC CARBONATE SEDIMENT COLOR AND OCEAN OXYGENATION

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ABSTRACT

One of the oldest observations in geology is that Paleozoic carbonates are reduced colors—grey and black—while Mesozoic and younger carbonates are oxidized and typically white or tan yet this observation has never been quantified or explained. Our survey of 850 carbonates over the past 500 Ma verifies that there is a strong secular trend in which the first tan-white carbonates appear about ~200 Ma ago and largely displace grey carbonates by 100 Ma—a pattern we contend reflects the history of ocean oxygenation. Grey carbonates, like those in the Paleozoic, reflect conditions of excess organic matter and other reducing agents relative to oxygen, while the reverse is true in white or tan carbonates. We infer that Paleozoic carbonates are nearly always grey because high organic matter production in epicontinental seas caused water column O_2 to be largely consumed by heterotophs even during times of hyperoxia in the Devonian and Carboniferous. The disappearance of large epicontinental seas in the early Mesozoic and increases in burrowing intensity of post-Paleozoic infauna reduced organic matter burial rates and contributed to the widespread appearance of oxidized marine carbonates. The nearly complete oxidation of even deep sea carbonates starting at 100 Ma reflects further increases in burrowing intensity and the rise of ballasting skeletonized plankton that increased the efficiency of organic matter export from the surface oceans. Our findings are in agreement with records of I/Ca as well as evidence from animal body size, bioturbation intensity and animal motility that all suggest that ocean oxygen concentrations rose to near-modern levels about 200 million years ago. Atmospheric oxygen reconstructions from these proxies, however, may be skewed towards lower oxygen concentrations in the Paleozoic due to the prevalence of epicontinental sea sediments during this interval that were subject to inefficient ballasting from skeletal remains and low rates of bioturbation by infauna.

1. INTRODUCTION

In the 1830's German geologists noticed that many of the oldest rocks in the Schwäbische Alb, the "Black Jurassic", were overlain by the younger, "White Jurassic". This observation was later identified as a part of a global secular trend from grey Paleozoic carbonates to white Mesozoic carbonates (Ager, 1973). The color of marine carbonates, like those in the Schwäbische Alb, reflects changes in the balance between the production of organic matter, its consumption by oxygen-using microbes and invertebrates, and overall exposure time to oxygen in the water column. When sedimentary organic matter is so abundant that all oxygen is consumed, microbial communities switch to anaerobic metabolisms and catalyze reactions that produce reduced minerals that turn sediments grey or black. When oxygen is abundant, such that reduced phases completely oxidized, sediments are typically white, tan or red. Therefore, color is an indicator of changing oxygen concentrations directly linked to organic matter and iron oxidation in the marine environment ((Lyle, 1983)). Black shales, for instance, reflect excess organic matter and metal-reducing capacity in the sediment relative to available pore water oxygen, but may also reflect low water column O_2 concentrations (as in Cretaceous Ocean Anoxic Events) or a combination of mid water hypoxia and high organic matter production as in Mediterranean sapropels (Brumsack, 2006; Filippelli et al., 2003; H. C. Jenkyns, 1980; Hugh C. Jenkyns, 2010a; Passier et al., 1999; Rohling, 1994; Song et al., 2017)). Most quantitative models of paleo-oxygenation that are based on marine sediments such as molybdenum isotopes and, more recently, I/Ca ratios, also primarily track some combination of pore water and water column O_2 concentrations relative to reducing agents. Hence, most marine sedimentary geochemical systems, including sediment color, estimate oceanic dissolved O_2.

2. METHODS

Samples were collected from a combination of outcrop samples with well-characterized, published stratigraphy and samples located in collections facilities with existing age constraints. Outcrop samples were collected at frequency high enough to capture color variations in bedding planes in all outcrops, approximately every 0.5 to 2 meters depending on section stratigraphy. Signs of diagenetic alteration that were used as rejection criteria included weathering rinds, fracturing, recrystallization, dissolution textures, and hydrothermal alteration. Depositional environments in most cases were categorized via existing literature and in other cases through examination of hand samples. Categorization of individual hand samples from collections facilities was based upon grain size, percent of fossils in matrix, or literature related to sample formations. Data within the manuscript were plotted at 700nm to show the secular trends in sediment color more clearly, however the same pattern appears across the entire visible light spectrum (See Appendix A for Figure 10, Figure 11). Raw reflectance spectra of samples (see Appendix A for Figure 12) shows that light, grey, black samples (top, middle, and bottom lines respectively) have substantially different reflectance profiles across all wavelengths of visible light.

Additionally, DSDP/ODP/IODP data were used to supplement hand sample data in the Cenozoic. Spectrophotometric data at the 700nm wavelength band were utilized from two carbonate rich (> 50% $CaCO_3$) ODP sites (Leg 198 site 1210A and Leg 208 site 1263A) were selected at random two million year intervals. Simple biostratigraphic age models for each site were constructed via microfossil data openly available on GeoMapApp (http://www.geomapapp.org). Biostratigraphically constrained tie points obtained from GeoMapApp were linearly interpolated to create the age model for both sites.

3. RESULTS

We measured the color reflectance in marine carbonate samples over the last 541 Ma from reef and tidal flat environments to the deep sea. In the Paleozoic, carbonates from all marine environments are almost exclusively shades of grey (5 to ~30% reflectance) with the exceptions being occasional cases of very slowly accumulating red and brown clay (with ~40% reflectance). The first high-reflectance (white to yellow; up to 85% reflectance) carbonates appear abruptly at about 200 Ma in inner shelf carbonates. By 150 Ma the first white pelagic chalks appear with >70% reflectance and then, about 100 million years ago, even deep-sea chalks become dominantly oxidized and the abundance of reduced carbonates becomes rare in all environments. Carbonates from the last 50 Ma sampled by scientific ocean drilling show a similarly high variation in sediment reflectance ranging from grey to white even within individual cores (Diester-Haass et al., 2004; Giosan et al., 2002) but reduced colors are uncommon.

4. DISCUSSION

Sediment color is initially set during early diagenesis either by formation of reduced mineral phases or their absence (21). During late diagenesis reduced colors are difficult to produce in already lithified oxidized rocks because the reactants (particularly organic matter and oxygen) are usually in short supply. The major drivers of sediment color include organic matter abundance and redox state of iron (and sometimes manganese) within the sediments (Myrow, 2003). Both variables respond to changes in organic matter production and consumption in the water column as well as sedimentation rates, availability of Fe and Mn as oxygen sinks, and biological processes such as sediment irrigation by burrows and consumption of sedimentary organic carbon by microbes and burrowing animals. Preservation of both organic matter and redox state of iron within sediments are therefore tightly linked and interactions between these components often occur throughout early diagenesis of marine sediments (Robert A Berner, 1984; Henrichs, 1992; Lalonde et al., 2012; Meyers, 2007). Degradation of organic matter occurs in marine sediments in order of reactants that result in maximum free energy yield (Donald E. Canfield, 1993). Heterotrophy is the most efficient metabolism in terms of free energy yield, so oxygen is utilized until it is entirely consumed. Once oxygen has been depleted, bacterial sulfate reduction takes over as one of the next most efficient metabolisms. Bacterial sulfate reduction produces hydrogen sulfide (Robert A Berner, 1984; Bowles et al., 2014) which, in the presence of iron oxides (hematite, goethite, lepridocite, and ferrihydrite), react rapidly in the presence of sulfate in pore waters to form pyrite (Donald E. Canfield, 1989; Raiswell & Canfield, 1998). Carbonates that have sufficient organic matter for microbes to completely consume available oxygen and drive sulfate reduction will become grey or green through the accumulation of pyrite and other reduced phases, while sediments whose organic matter is entirely consumed by oxidative reactions early in diagenesis will have oxidized forms of iron and be shades of white, yellow or red.

4.1. SULFATE CONCENTRATIONS

Low sulfate or reactive iron concentrations may inhibit bacterial sulfate reduction (Robert A Berner, 1984; Raiswell & Canfield, 1998; Westrich & Berner, 1984). Still, sulfate concentrations are rarely rate-limiting to pyrite formation in most marine sediments above the ~5 mM concentrations estimated to have been exceeded since the Ediacaran to mid-Cambrian (Algeo et al., 2015; Berner, 1984; D. E. Canfield & Farquhar, 2009). Additionally, while concentrations of reactive iron may inhibit pyrite formation in Precambrian marine sediments, the oldest samples in our record are dark grey (Figure 1E), indicating that reactive iron limitation did not prevent iron reduction in the last 500 Ma (Canfield, 1989). Weight percent of reactive iron also does not vary greatly between continental margin and deep-sea sediments (Raiswell & Canfield, 1998). Hence, the abundance of marine sulfate and reactive iron is unlikely to produce the trends in sediment color observed here.

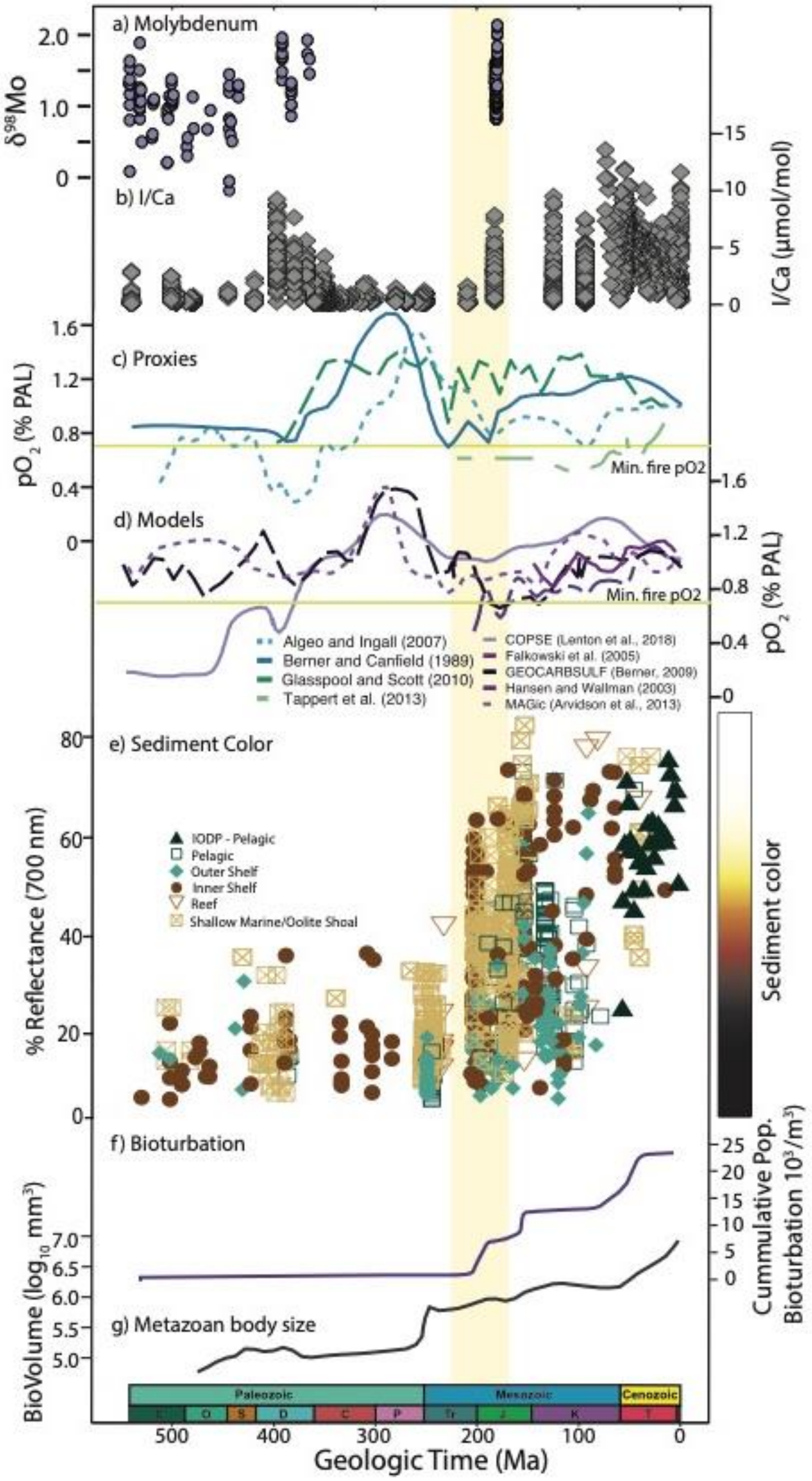

Figure 1 – A) Molybenum isotopic data suggests Devonian oxygenation of deep sea. B) I/Ca data indicate initial oxygenation during Devonian, followed by subsequent rise of oxygen at 390 ~200 Ma. C) Proxy inversion models of Phanerozoic atmospheric pO2. D) Isotope Mass Balance (IMB) models of atmospheric oxygen E) Carbonate sediment reflectance data. Red horizontal bar indicates transition zone from black sediment to white sediments. F) Qualitative bioturbation rates across Phanerozoic time. G, 95 percentile metazoan biovolume.

4.2. PRIMARY PRODUCTION

Biological productivity, in contrast, can dramatically affect sediment color by regulating the abundance of sedimentary organic carbon--a key reactant in the consumption of oxygen by microbes and infaunal invertebrates. For example, high export productivity promotes the complete consumption of oxygen in the water column or in seafloor sediments and promotes formation of reduced iron phases in diagenesis. Low export production, in contrast, can preserve sufficient oxygen to fully oxidize sedimentary iron (Bertrand & Lallier-Vergès, 1993; Cai & Sayles, 1996; Calvert, 1987; Donald E. Canfield, 1994; Jørgensen, 1982). Sedimentary organic carbon content is also affected by oxygen availability in the water column. As the ocean becomes better oxygenated, more organic carbon is consumed in the water column, limiting the rain rate of organic matter to the sea floor. At the same time, the evolution of mineralizing plankton can increase the ballasting of organic matter flocs, and hence carbon export, while helping maintain oxygen inventories in the water column. Hence, sedimentary color is driven to oxidized colors both by extensive organic matter remineralization in the water column and sediments.

4.3. SEDIMENTATION RATE

Sedimentation rate affects sediment color by varying the exposure time of organic carbon to oxygenated bottom waters at the water-sediment interface. Slow burial in the presence of oxic bottom waters results in complete consumption of organic carbon and the formation of red, yellow or white oxidized sediments (Hartnett et al., 1998) where long exposure times allow oxidation of iron phases on the seafloor. Low sedimentation rates account for the examples of reddish or brown carbonates (with nearly 40% reflectance) observed throughout the Phanerozoic.

4.4. WEATHERING

Once sedimentary organic matter has been consumed by heterotrophy, there is no organic matter left to be utilized by bacterial sulfate reduction or other anaerobic metabolisms so oxidized sediment is difficult to turn into reduced sediment. Instead, weathering drives progressive oxidation of reduced iron and decomposition of organic matter and should lead to progressive lightening of carbonates upon long exposure resulting in brown, orange, red, and yellow weathering rinds on otherwise grey rocks. Therefore, grey colors in unweathered Paleozoic rocks must reflect the original dominance of reducing conditions near the seafloor. Sedimentary rocks with primary oxidized colors are a distinctly Mesozoic and Cenozoic phenomenon. Indeed, if weathering were a dominant feature of carbonate rock color, then we would expect many more oxidized Paleozoic rocks than we find. Furthermore, fresh carbonates recovered in ocean drill cores and quarries include white and cream-colored carbonates despite the absence of surface weathering. Hence, weathering is not sufficient to explain the abrupt transition in sediment color we observe at ~203 Ma.

4.5. PALEOZOIC EPICONTINENTAL SEAS

We suggest that the reduced colors are typical of Paleozoic carbonates because most of the sedimentary record is that of shallow, highly productive epicontinental seas where organic matter was originally abundant, and irrigation by benthic burrowers was weak. Today, epicontinental seas like the Gulf of Carpentaria, the North Sea, and Persian Gulf are highly productive environments with abundant chlorophyll as seen from estimates derived from satellite sea surface color. For example, tropical epeiric seas, such as the Java Sea, have productivity levels that are among the highest in the oceans. Sediment cores reveal that total organic carbon within modern epeiric sea sediments commonly reach 2-13%. Both modern and ancient epicontinental seas experience also frequent hypoxic events because of freshwater runoff and nutrient inputs from land, and these also drive up the reducing capacity in such environments (Allison & Wells, 2006). The shift to oxidized carbonates we observe in the Mesozoic partly reflects the disappearance of highly productive epicontinental seas due to the tectonic assembly of Pangea. Nearly all of our marine record in the Paleozoic comes from epicontinental seas. As highly productive basins, Paleozoic epicontinental seas are likely to produce hypoxia or even anoxia in sediments regardless of oxygen concentration in the atmosphere (Algeo et al., 2008). Hence, it is not surprising that our carbonate color record as well as many other geochemical proxy systems based on marine sediments record low dissolved oxygen levels, and singularly fail to show the late Paleozoic episode of atmospheric hyperoxia suggested by some Earth System models.

4.6. BIOTURBATION

Improved irrigation of marine sediments by burrowing animals is also likely to contribute to the appearance of well oxidized carbonates in the Mesozoic. Burrowing generally results in decreased concentrations of sediment organic matter (Aller, 1994; R. A. Berner & Westrich, 1985; Kristensen, 2000; van de Velde & Meysman, 2016) through direct consumption of organic matter and infiltration of oxygenated water from the overlying water column. While sedimentary fabrics are first completely disrupted in the Ordovician (Droser & Bottjer, 1989) (when carbonates are nearly always reduced colors), both the depth of burrowing and burrowing intensity were less than in the Mesozoic and Cenozoic resulting in incomplete consumption of organic matter. Rates of bioturbation rapidly increase during the mid-Mesozoic (Allmon & Martin, 2014b; Thayer, 1983) consistent with the replacement of dominantly sessile "Paleozoic-like" marine communities (Figure 2A) by Mesozoic fauna (Figure 2B) and eventually the highly mobile "Modern" fauna (Figure 2C) (*The Mesozoic Marine Revolution*, 2016; Harper, 2003; Geerat J. Vermeij, 1977b). In-situ studies today suggest decreasing bioturbation depth, bioturbation intensity, and burrow length are strongly linked to declining bottom-water oxygen concentrations in hypoxic zones (Sturdivant et al., 2012). Hence, the trend toward increased burrowing in the Mesozoic and Cenozoic is consistent both with a rise in seafloor O_2 content and the appearance of oxidized sediments.

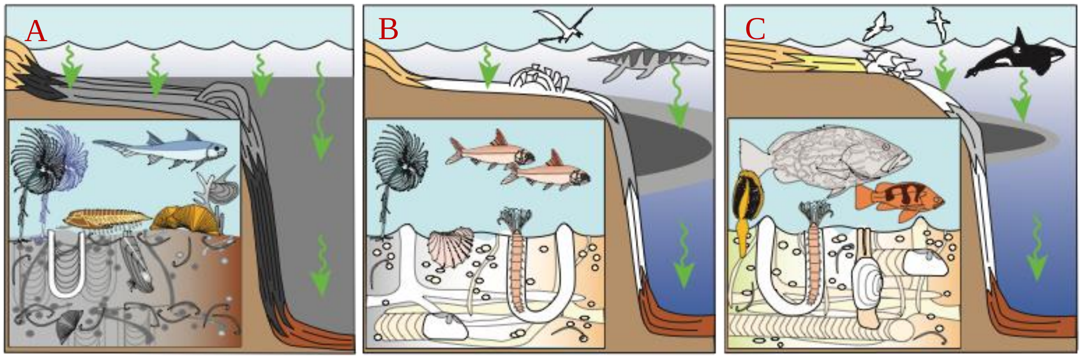

Figure 2 – Graphical representation of Paleozoic, Mesozoic, and Cenozoic ocean oxygen concentrations and marine community structure. A) Paleozoic oceans were characterized by relatively sessile, small bodied organisms requiring minimal amounts of oxygen and primary production. Widespread hypoxia and incomplete organic matter remineralization led to pervasive reduced, dark carbonate sediments found from shallow mudflat environments to outer shelf depositional environments. B) Rising oxygen concentrations in the Jurassic led to increasingly active fauna both in the water column and in the sediment. Increased pO2 in the water column generated oxidized, light sediments except in the presence of substantial O2 minima where reduced sediments formed. Increased bioturbation rates relative to the Paleozoic contributed to extensive oxidation of carbonate sediments through consumption and aerobic respiration of organic matter. C) Cenozoic communities became more energetic than in earlier times, characterized by increased activity and modern predator-prey relationships. High bioturbation rates and nearly complete water column consumption of organic matter led to oxidized, light-colored sediments other than in areas associated with O2 minima.

5. CONCLUSION

Our results agree broadly with marine proxy systems for O_2 but have large discrepancies with Earth system models that predict atmospheric pO_2. For instance, molybdenum isotope data coupled with cerium anomaly data for marine sediments have been interpreted to suggest low levels of early-to-middle Paleozoic pO_2 (15-50% PAL) and I/Ca records support generally low pO_2 in the Paleozoic until the early Jurassic; both proxy systems are broadly in agreement with our sediment color evidence for dominantly hypoxic marine pore waters in the Paleozoic. At the same time, both Mo isotopes and I/Ca suggest a transient rise in pO_2 in the Devonian which we do not observe in the color reflectance record, possibly because our record reflects pore water O2 whereas other geochemical proxies capture primarily water column signals. Terrestrial proxy data diverge from most marine-based O_2 proxy systems in the mid Paleozoic. For example, evidence for fire in forest duff, suggests atmospheric oxygen concentration exceeded ~0.7% PAL by the Middle Paleozoic (Belcher & McElwain, 2008) and Earth system models sometimes infer hyperoxia, with 1.6% PAL, associated with widespread coal deposition in the later Paleozoic, a phenomenon neither observed in Mo isotopes and I/Ca nor in our record.

We suggest that discrepancies between the timing of the carbonate color transitions and terrestrial proxies or Earth system models likely reflect decoupling of marine pore water O_2 and atmospheric pO_2. Even today, when atmospheric pO2 is 21%, the bottom of the Black Sea is anoxic and other marginal seas like the Sea of Japan, the Mediterranean, and the Baltic have all been rendered hypoxic through a combination of freshwater flux and nutrient delivery from land. Similar mismatches between the atmosphere and ocean are expected in epicontinental sea environments that have high amounts of freshwater influx and nutrient input from surrounding landmass. The dominance of hypoxic epicontinental seas in the Paleozoic sediment record suggests that geochemical measurements made on sediment phases such as bulk carbonate or benthic invertebrate skeletons are likely to carry an oceanic bias. When the record switches to late Mesozoic/Cenozoic samples more representative of open ocean environments, an abrupt shift occurs where oxidized sediments subject to lower concentrations of organic matter delivery, increased irrigation of sediments as bioturbation rates increase, and higher water-column oxygen levels, begin to appear. The nature of this transition began in shallow marine environments (~200 Mya) about 100 million years before becoming widespread in pelagic carbonates. Therefore, we suggest that increasing dissolved oxygen concentrations and rising [O2] across all zones of the ocean (relative to Paleozoic epicontinental seas) is a more likely driver of the step changes at ~200

Ma than deepening of the oxycline alone. Rising oxygen concentrations at ~200 Ma are supported by experimental data of microbial sulfate reduction and sulfur isotopic fractionation data coupled to a biogeochemical model of pyrite burial (Leavitt et al., 2013). These data both suggest that pO_2 levels passed through a threshold rise at ~200 Ma, leading to a state shift in the marine system recorded in both sediment color and sulfur isotopic data.

Reconstructing atmospheric oxygen over geologic time is an important component to understanding nutrient regeneration in the water column, the evolution of life, and community energetics. Our record of carbonate sediment color, however, suggests that Phanerozoic reconstructions of atmospheric oxygen may be skewed by the prevalence of Paleozoic epicontinental seas that are often biased towards hypoxia. As a result, marine proxies used in the Paleozoic to infer global atmospheric oxygen conditions should be interpreted with caution. Modern epicontinental sea environments are subject to unique environmental conditions that represent substantial biotic and biogeochemical differences from open ocean environments. Modern epicontinental seas also differ from their Paleozoic analogs. They are characterized by efficient ballasting and high burrowing intensity that were absent in epicontinental sea environments until the evolutionary radiations of the Mesozoic Marine Revolution. It is therefore no surprise that substantial differences exist between marine proxy systems that indicate low Paleozoic O_2 compared to terrestrial proxies from pO_2 and Earth system models. The switch to high pO_2 in the Mesozoic may be a result of these changes, such as decrease in area of epicontinental seas and increases in bioturbation efficiency and organic matter export efficiency by ballasting sinking organic matter with mineral skeletons. Our data suggest that even if Paleozoic oxygen partial pressure in the atmosphere exceeded modern, such as in the Carboniferous, the unique paleogeography of many Paleozoic carbonate sediments may skew the data towards lower marine oxygen concentrations.

ACKNOWLEDGEMENTS

DSDP/ODP/IODP data were generously provided by the International Ocean Discovery Program. We thank Scripps Institution of Oceanography and the University of Heidelberg for access to collections facilities and samples. R.K.S is funded by the National Science Foundation Graduate Research Fellowship Program. R.D.N. is funded by Scripps Institution of Oceanography and DFG Projektbüro Exzellenzinitiative Research Fellowship of the State of Baden Württemberg and Heidelberg Universität. J.P. and O.F. are funded by the University of Heidelberg.

Chapter two has been submitted for publication and is in review in Science Advances and will appear as: Sugla, R. K., Friedrich, O., Pröss, N. M., Norris, R.D. Secular trends in Phanerozoic carbonate sediment color. Science Advances. (2021). The dissertation author was the primary investigator and author of this paper.

CHAPTER 3

INCREASED METABOLIC DEMAND IN THE MESOZOIC MARINE REVOLUTION TRACKS RISING OCEAN OXYGEN CONCENTRATIONS

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ABSTRACT

Sessile and slow-moving marine animal clades with Paleozoic originations were replaced by metabolically active, highly mobile fauna in the aftermath of Permian-Triassic mass extinction. Paleozoic groups were displaced from warm, shallow marine environments by Mesozoic and Cenozic clades with origins in the last 100-200 million years. This change-over in animal ecologies has been called the Mesozoic Marine Revolution and is reflected in everything from predation intensities to bioturbation. Here, we use a large database of over 20,000 modern vertebrate and invertebrate metabolic rates combined with molecular clock data to create a record of energetic demands during the last ~500 million years. Our study assumes that there has been phylogenetic conservatism in metabolic evolution following the evolutionary appearance of each clade. Under an assumption of phylogenetic conservatism, metabolic rates normalized for body mass do not change systematically over time. This result is expected since specific metabolic rates (per gram of tissue) are substantially set by the basic body form and respiratory system of each clade. However, there is a distinct increase in body mass over time and this drives a need for more metabolic energy. Indeed, we find a five orders of magnitude increase in maximum metabolic energy utilization over the Phanerozoic as body sizes increase among many groups of marine animals. Maximum body mass and energy needs increase particularly quickly in the early

Mesozoic (~200 Ma) synchronous with independent evidence for an increase in ocean oxygenation.

1. INTRODUCTION

The Mesozoic Marine Revolution (MMR) was a rapid ecological and behavioral transition in marine ecosystems that was reshaped by complex predator-prey relationships (Vermeij, 1983; Vermeij, 1977a, 2013), increased rates of burrowing and bioturbation (Thayer, 1979, 1983), infaunal tiering (Ausich & Bottjer, 1982; Bottjer & Ausich, 1986), the radiation of primary producers (Falkowski & Knoll, 2007) and novel predation strategies (Oji et al., 2003; Salamon et al., 2020).The most commonly cited driving factor for the MMR is the radiation of large primary producers which increased the availability of trophic resources (Falkowski, 2005; Falkowski et al., 2004). Unlike other periods of rapid evolutionary change, such as the rise of eukaryotic life and the Cambrian explosion (Sperling et al., 2013; Sperling et al., 2015) however, the MMR is generally not directly linked to changing oceanic oxygen concentrations. More recent data, however, provide compelling evidence for rising oxygen concentrations in both the water column and the sediment-water interface at ~ 200 Ma (Lu et al., 2018). As a result, the links between oxygen, nutrient availability, and the onset of the Mesozoic Marine Revolution must be explored in greater detail.

Previous attempts to quantify macroevolutionary energetic trends throughout the Phanerozoic have been limited by the temporal resolution of the palaeobiological record and our ability to estimate metabolic rates of species found in the fossil record. Early estimates of energetic trends qualitatively characterized Paleozoic, Mesozoic, and Cenozoic communities through inference of predation strategy, morphology of fossils, or anti-predation strategies evident from defensive structures in fossil specimens (Vermeij, 1983) Recent studies utilize body size estimates of fossil specimens (Finnegan et al., 2011; Heim & Knope, 2015; Payne et al., 2011) and allometric scaling principles derived from extant taxa to estimate metabolic rates.

Quantitative energetic data with high temporal resolution are necessary to accurately reconstruct Phanerozoic energetic trends and understand potential links between changing nutrient availability, oxygen concentrations, and the Mesozoic Marine Revolution. We integrate both needs by utilizing a large database of invertebrate and vertebrate metabolic rates of over 20,000 lab and in-situ respiration rate measurements from ~1000 different species. We then examined the distribution of these metabolic data over the Phanerozoic using phylogenetic trees calibrated via molecular clocks.

2. METHODS

Respiration data were collected through literature review, existing compilations of metabolic data, personal communications, and online databases such as Fishbase (Froese, R. and Pauly, D. (2020)) or such as in Brey, 2001. Data presented here represents a mixture of in situ and laboratory-based respiration measurements. Each set of measurements was checked to ensure that procedures and equipment utilized were explicitly listed. Only data with body mass measurements, taxonomic information, and the respiration measurements setup (such as sensor, temperature of measurements, and respirometry system type) were utilized. See Table 1, Appendix B for taxonomic breakdown of data.

Additional criteria for the data included that only measurements with experimental temperatures within that of annual habitat range, that experimental temperatures were not +/- 50% of the temperature at which the organism was caught, and that all organisms were acclimatized prior to experimental measurements if temperatures were greater or less than the temperature at which the organism was caught. Wherever possible, additional data were included (environment, feeding type, habitat depth).

Metabolic rates were converted to the same units (J J^{-1} D^{-1}) as conversion factors defined in previous studies (Brey, 2001). Where possible, species-specific conversion factors were utilized and, where unavailable, averaged conversions factors based on an organism's taxonomic membership were obtained from the databank and utilized instead (Brey, 2001).

In order to compare metabolic rates across time, respiration rates were normalized to the same temperature (15°C) by using the Arrhenius equation (J. H. Brown et al., 2004a).The combined effects of body mass and temperature on metabolism are described through:

$$R = a * M^b * e^{\frac{-E}{(k*T)}} \qquad (1)$$

Where R is respiration, M is body mass, b is the metabolic scaling coefficient, E is activation energy, k is the ratio of gas constant to the Avogadro constant and T is temperature in Kelvin. When log transformed, this can be rearranged and used to normalize metabolic rates to the same temperature using a multiple regression:

$$\log\left(\frac{R}{M}\right) = \log(a') + (b_1 - 1) * \log(M) + \frac{b_2}{T} \quad (2)$$

Regressions for this analysis were done with data at the highest taxonomic resolution possible. Taxonomic data, when not already provided, were collected through the *rfishbase* API or the *Integrated Taxonomic Information System*. Regressions for temperature normalization were done at the highest taxonomic rank for which sufficient data were available to run the regression. For example, if sufficient data were available, metabolic rates were normalized at the genus level. If insufficient amounts of data were available at the genus level, regression coefficients were determined through a second set of regressions conducted at the family level, and subsequently order level, class level, etc. For most data in the study (>90%), regression coefficients were determined at the family level.

Taxonomic position was utilized to determine first appearance dates in the fossil record. For hard-bodied taxa with extensive fossil records, the *Paleobiology Database* was used to determine first appearance dates. Invertebrate taxa without distinct skeletal remains and other taxa with poor fossil records were dated using molecular clock data found through literature review or best estimates from databases such as *www.timetree.org.* Wherever possible, first appearance dates were determined at the genus level. In cases where genus-level data were not available, family or order level first appearance dates were utilized. For groups with poorly constrained molecular clock and fossil dates due to lack of easily fossilized structures, such as sponges and jellyfish, class level dates were used.

Occurrence data were obtained through the paleobiology database. Occurrence data for bivalve and modern fish groups (Acanthodii", Actinopteri, Actinopterygii, Chondrichthyes, Cladistia, Osteichthyes, and Plagiostomi) followed methods described in (Kocsis et al., 2019) and (Kocsis et al., 2018.). Size data for bivalves and bony fish groups were obtained from previous compilations of marine body size across Phanerozoic time (Payne et al., 2014; Payne & Heim, 2020).

3. RESULTS

We use a database of over 20,000 respiration measurements combined with molecular clock data to estimate changes in community level metabolic rates over the past 541 million years. Mass-specific metabolic rates per unit mass of organisms vary between -3 to -0.5 log(J/J/D) metabolic rates across the entirety of the Phanerozoic with no distinct trend (Figure 3A). Metabolic rates of entire organisms span a higher range, from -4 to +10 log(J/J/D) from the early Paleozoic to the early Mesozoic (541 – 180 Mya) (Figure 3B). The minimum metabolic rate (constant at ~4) remains approximately constant over the whole record. However, starting about ~ 175 Ma, the maximum range of metabolic rates begins to increase from about +4 in the Paleozoic to +8 log(J/J/D) at ~ 125 Ma and in the mid to late Cenozoic (25 Ma – present) (Figure 3B).

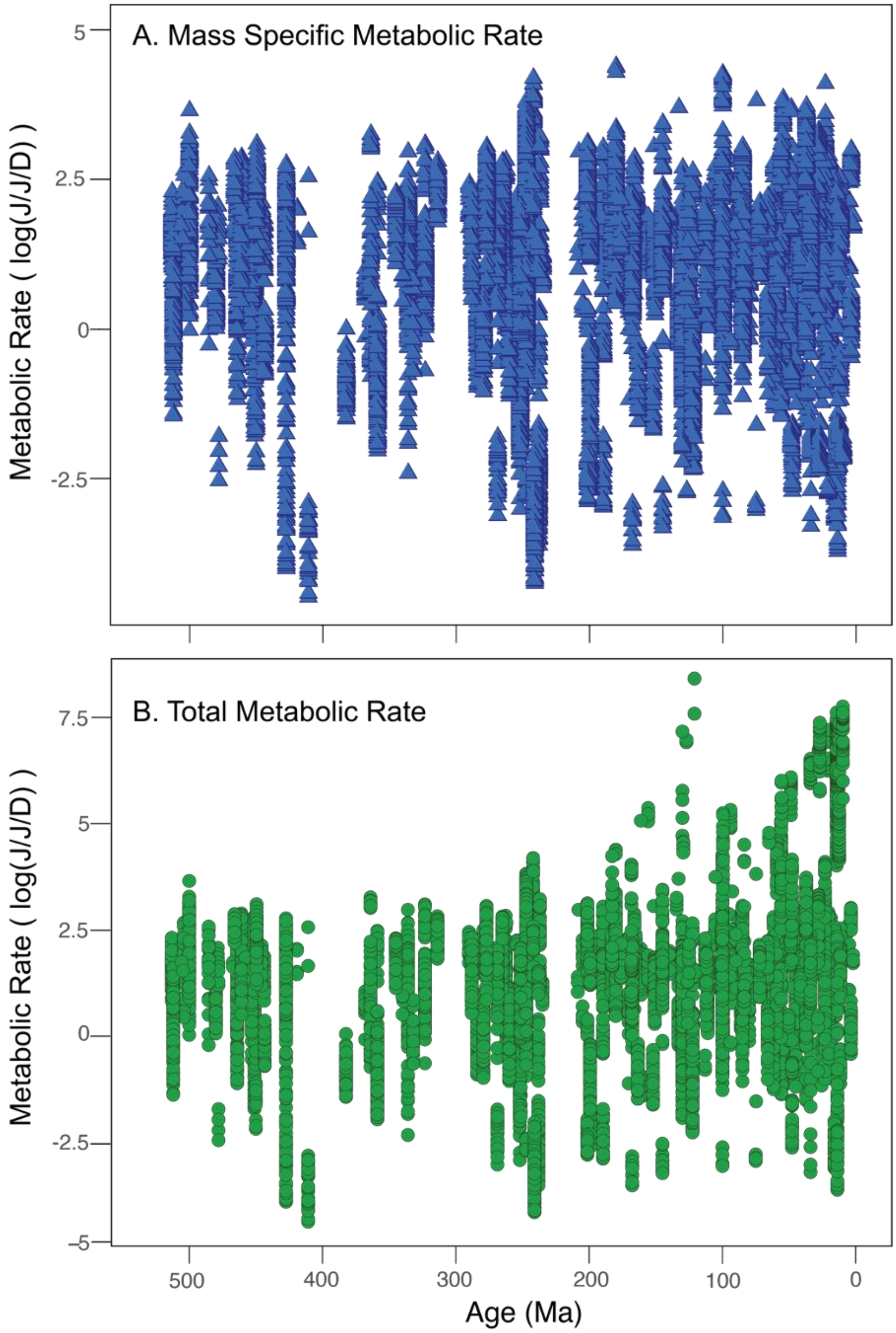

Figure 3 – A) Mass-specific metabolic rates plotted against time indicate indicate metabolic rates per unit mass of organisms remain steady across a constant range throughout the Phanerozoic. B) Metabolic rates of whole organisms suggest distinct changes in activity levels during the Mesozoic Marine Revolution. This suggests that changing environmental conditions may have relaxed constraints on body size and allowed for radiations of large, metabolically active organisms in the past ~150 Ma.

The increase in metabolic rates of entire organisms largely reflects the impact of the "Mesozoic fauna", such as much of modern day Cephalopoda, Bivalvia, Gastropoda, Elasmobranchii, and Teleosti. Metabolic and occurrence data of bivalves, for example, shows both increasing numbers of occurrences in the fossil record and step-changes towards higher metabolic rates in the early Mesozoic (Figure 4). Modern bony-fish data show a similar trend of increasing body size and rates of occurrences in the fossil record.

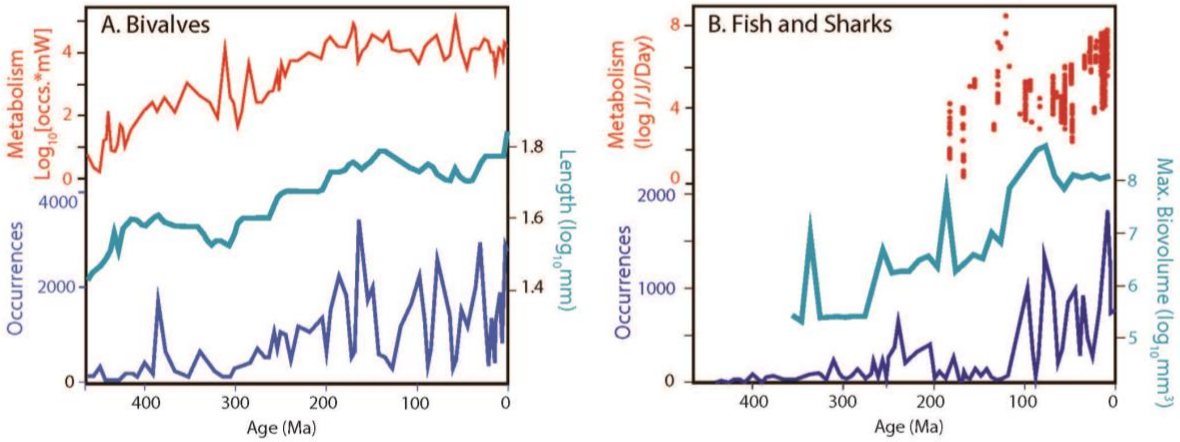

Figure 4 – Metabolic rates, size, and occurrence data for (A.) Bivalves and (B.) Fish and Sharks. Solid red curve/dots at the top of the charts show rising metabolic rates towards the present. Middle light blue curves show increasing size for both bivalves and modern bony and cartilaginous fish. Bottom dark blue curves show occurrence data obtained for each group.

4. DISCUSSION

Previous research indicates mass-specific metabolic rates are constrained within a relatively narrow window across all of life's domains (Makarieva et al., 2008). Constraints range from the metabolic optimums or by physiological limitations imposed by eukaryotic cells within organisms (Hatton et al., 2019; Makarieva et al., 2008) as well as the oxygen supply mechanisms associated with an animal's body plan. Our data supports this and indicates that regardless of when families of modern clades originated, mass specific metabolic rates were constrained within such a window. The +1 to -4 log(J/J/D) range in mass-specific metabolic rates is clear despite the variation in habitats, activity levels, and body plans across the Phanerozoic (Figure 3A). The lack of trend in mass specified metabolic rates is important, as it suggests that animals acquired characteristic metabolic efficiencies early in the evolution of the various clades. Although it is clear that animal metabolic rate adjusts to changing temperature, O_2 availability and activity levels by changes in behavior, and adaptations such as thicker, or larger gills, these adjustments occur within a set of basic anatomical constraints that were reached early in evolution and have been maintained over most of the Phanerozoic.

For instance, oxygen limitation can be dealt with through compensatory mechanisms that increase oxygen supply when environment pO2 declines (Deutsch et al., 2020). An example is an organism that spends the majority of time in the shallowest part of the water column where wind-driven mixing facilitates better-oxygenated waters from gas exchange with the atmosphere. Organisms may also increase respiratory surface area relative to body size to increase oxygen supply in oxygen-poor waters, a common strategy employed by mesopelagic fish in oxygen minimum zones today (Seibel & Deutsch, 2020). In some cases, modern deep-sea fish in oxygen limited waters have employed strategies such as having gills large enough that they emerge from the opercula.

Alternate strategies also include raising hemoglobin levels to increase oxygen supply within the circulatory system in poorly oxygenated waters or storing oxygen in body mass (i.e. increasing muscle oxidative capacity) for higher activity periods, while other midwater fish are gelatinous, or have minimal activity other than burst swimming. Many modern marine megafauna also employ strategies that involve temporary migration from oxygenated waters into the oxygen minimum zone environments to feed or to escape predation (Seibel, 2011). Some, like elephant seals, directly access the atmosphere for O2 and use that for unrestricted movement in the OMZ--

a strategy not possible in vertebrates until the evolution of ichthyosaurs and Devonian lungfish (Clement & Long, 2010; Naito et al., 2017).

Although there are numerous mechanisms that organisms can use to maintain their specific metabolic rates, the situation changes as animals increase body size and therefore metabolic demand. Metabolic rates of organisms scale to body size and temperature through the allometric scaling relationships described through the Metabolic Theory of Ecology (J. H. Brown et al., 2004a; J. F. Gillooly et al., 2001; James F. Gillooly et al., 2016). According to this theory, metabolic rates exponentially scale with temperature (described through the Arrhenius-Boltzmann equation) and scale to body mass ~ $M^{3/4}$. While this relationship is modulated by ambient environmental temperature, particularly in marine ectotherms that match internal temperatures to that of the surrounding environment, this pronounced increase in body size persists across hothouse and icehouse conditions in the Phanerozoic and suggests a trend towards increasing community metabolic demands despite varying marine temperatures.

Evidence suggests that *individual* species may be limited in their capacity to maintain oxygen supply in low pO2 environments at large body sizes (Verberk et al., 2011). Mechanistic models and empirical data that represent oxygen transport from the physical environments into organismal respiratory pathways suggest that large body size, particularly in organisms with active lifestyles or those that live in warm environments, are susceptible to size limitation from low oxygen concentrations (Rubalcaba, Verberk, Hendriks, et al., 2020). This is partially due to the costs associated with physiological mechanisms to increase oxygen supply at large body sizes and active physiologies in the face of many potential rate-limiting steps in respiratory pathways. In modern oceans, organisms with life histories within hypoxic environments must develop increased oxygen supply capacities to maintain maximum metabolic rate similar to that of organisms in normoxic conditions, which may come at the expense of being able to develop larger body size. Resting metabolic rates are also more sensitive to environmental temperature changes than maximum metabolic rates, which appear to have a different allometric scaling relationship to body size than that of resting rates. At high temperatures, maximum metabolic rate may plateau due to oxygen limitations (i.e. capping out at the prevailing environmental pO2) while resting metabolic rates continue to increase, thus reducing aerobic scope of organisms. All organisms must maintain a minimum aerobic scope to maintain activities necessary for survival and reproduction. Aerobic scope may similarly be reduced during high activity periods. In fish, even activities such as eating which take up aerobic scope, may be halted to retain aerobic capacity (Norin & Clark, 2017). As such, large organisms may be able to persist in low oxygen environments, but selection may act as a pressure against this. At high temperatures, the temperature-driven increase in metabolism will force active or large organisms to have lower aerobic scope and lower hypoxia tolerance (Seibel & Deutsch, 2020).

The impacts of hypoxia tolerance from large body size are relevant to macroevolutionary trends across the Phanerozoic as body size is a heritable trait (Lind et al., 2015; Smith et al., 1995). Despite the fact that respiration data of extant taxa are used here, the strong phylogenetic conservatism of body size suggests that differences in resting metabolic rates of organisms should broadly persist through time. Biovolume estimates of marine fauna throughout the Phanerozoic, for example, show systemic variations in body size between different groups since the onset of the Mesozoic Marine Revolution (Figure 5) (Heim et al., 2020).

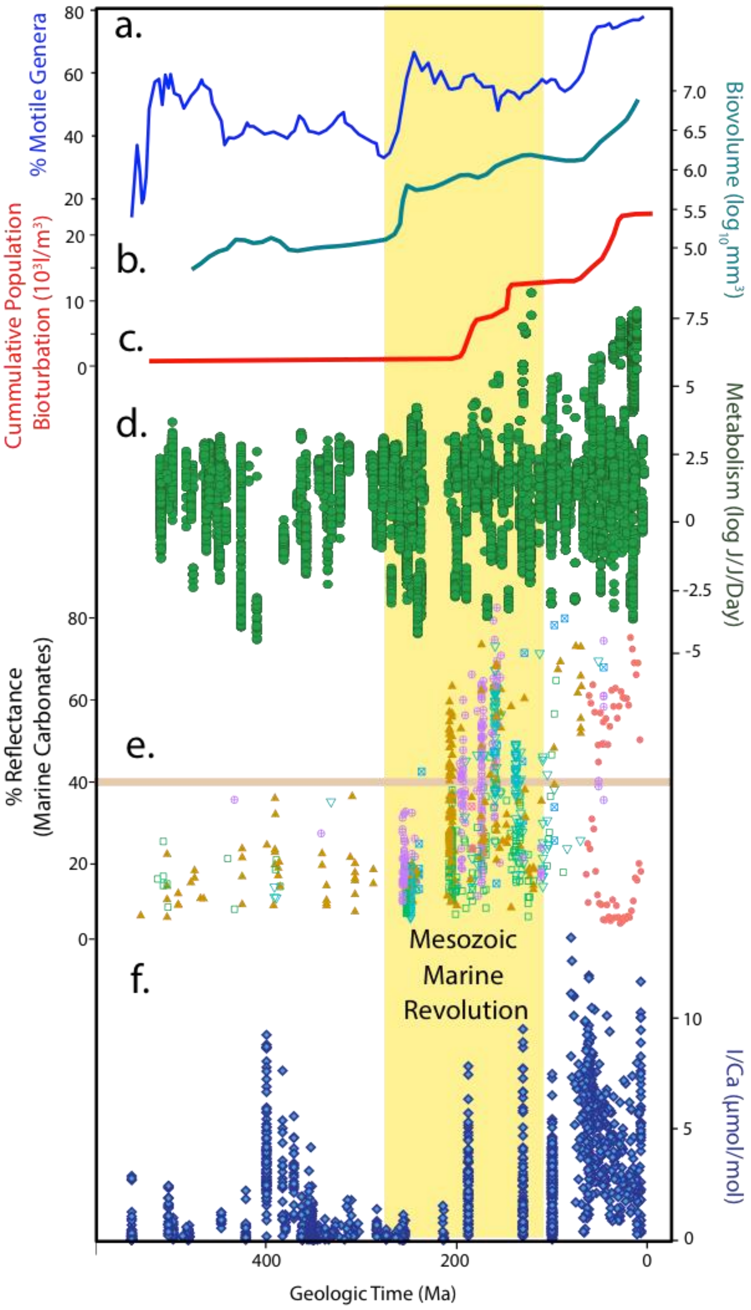

Figure 5 – Data from a wide variety of paleontological and geochemical proxies suggest a change in oceanic oxygen concentrations decoupled from atmospheric oxygen estimates and increases in motility levels of fauna. A,B) Percentage of motile fauna and body size of marine metazoans both increase during the Mesozoic Marine Revolution (MMR). C) Qualitative bioturbation rates across Phanerozoic time show a trend towards increasing sediment reworking rates. D) Metabolic rates of organisms through Phanerozoic time indicate larger and more metabolically active organisms radiated as ocean oxygen partial pressure rose. E) Carbonate sediment reflectance data suggest progressive ocean oxygenation across all depositional environments. F) I/Ca data indicate initial oxygenation during Devonian, followed by subsequent rise of oxygen at ~200 Ma.

The relationship between large body size and hypoxia tolerance suggest that ocean oxygenation had a large impact on the upper size range of marine animals. We suggest that our data showing increasing metabolic demands across the Phanerozoic due to larger size implies that the Mesozoic Marine Revolution was driven by an increase in ocean oxygenation. One of the most direct observations of the MMR is the replacement of sessile clades of Paleozoic origin with more energetically and metabolically active fauna in the Mesozoic, particularly in shallow marine environments (Bush & Bambach, 2011b). Canonical research in the field of paleobiology tracks a diversification of predation strategies, greater ecospace utilization, deep burrowing, high sediment reworking rates, and increasing proportions of fast-moving, nektonic fauna during the MMR. This trend towards increasing motility also tracks two orders of magnitude increases in mean body-size of marine metazoans across the Phanerozoic (Figure 5) (Heim & Knope, 2015).

There are several lines of evidence for increasing ocean oxygen inventories during the Mesozoic Marine Revolution, one of which concerns the metabolic systems used by marine plankton. For example, the redox sensitive trace elements required by red algal lineages, such as molybdenum, are more readily available in oxic oceans, while Paleozoic groups of green algae favor trace elements such as iron present in higher concentrations in low oxygen environments. Likewise, the Mesozoic radiation of coccolitophores and diatoms both utilize RuBisCo that also appears to have selected for conditions that would reflect upper ocean oxygenation (Rickaby & Eason Hubbard, 2019). At the same time, these nutrient-rich planktonic groups have larger average body size which may have contributed to improved ventilation of the surface ocean through ballasting (Knoll & Follows, 2016a; Meyer et al., 2016).

Sediment color data from marine carbonates and I/Ca data also provide support for increasing oxygenation and ventilation of the oceans as a factor selecting for red algal lineages that are adapted to higher ocean oxygen conditions. I/Ca data, which generally tracks oxygenation in the upper ~100 meters of the water column suggests a pronounced change in water column oxygenation at ~ 200 Ma towards increasing oxygenation (Lu et al., 2010). The carbonate sediment color record, which broadly reflects organic carbon burial and oxygenation at the sediment-water interface also supports rising oxygen concentrations and increased organic matter consumption in the water and sediment column at ~ 200 Ma.

Both the I/Ca and sediment color data suggests that atmosphere pO2 may have been decoupled from ocean O_2 inventories (Figure 5) (Lu et al., 2018). Given that maximum metabolic rates are tightly coupled to prevailing oxygen partial pressures an organism experiences, it is important to note marine communities for much of the Paleozoic or Cenozoic may not have maximized oxygen supply capacity to atmospheric pO2, except for extremely shallow-marine environments that were persistently oxic. In modern oceans, for example, wind mixing equilibrates surfaces waters with the atmosphere and maximal metabolic rates are tuned to atmospheric pO_2. Many marine environments are not persistently in equilibrium with the atmosphere, however, and organisms would have maximal metabolic rates calibrated to the lowest oxygen conditions they persistently experienced. Mixed layers may also be shallower in more stratified environments, such as the Black Sea, where the mixed layer is 10-30 m or so, or in dead zones where high runoff and nutrient inputs may cause hypoxia, anoxia, or euxinia in very shallow waters. Modern epeiric seas also show distinctly different patterns in temperature, circulation, salinity, and nutrient delivery than open-ocean environments that lead to oxygen partial pressures that deviate from the atmosphere.

The case of epeiric seas is particularly relevant for understanding the macroevolutionary trends in the Phanerozoic, including the MMR. The geologic and fossil record for much of the Paleozoic was deposited in epeiric sea environments that appear to have frequently experienced hypoxia and anoxia events, particularly in the presence of lower atmospheric oxygen pO2 of the early Paleozoic (Judd et al., 2020). Sediment color data suggests that even in Paleozoic shallow marine environments, seafloor conditions were likely hypoxic enough to allow for reducing conditions in the sediment column.

In such an environment, large-sized Paleozoic organisms in the same order of magnitude as modern marine metazoans would be the exception, rather than the rule. Many of the largest Paleozoic marine animals (such as the fish, *Dunkleosteus*, or meter-sized eurypterids) would need physiological adaptations to compensate for low oxygen partial pressures in the water column as a result of such pronounced decoupling between ocean-atmosphere oxygen concentrations. Even in modern oceans, such adaptations come at a cost which represent ecological limits based on energy investment into mechanisms to maintain oxygen supply. The tradeoffs of such adaptations are particularly prevalent in larger organisms as they may require increased gill surface area relative to body size, larger transport distances from gills to internal respiratory structures, and reduction of boundary layer thickness in gill surfaces tissues.

Records of rising oxygen partial pressures in the Mesozoic and Cenozoic indicate size and activity limitations may have occurred due to low oxygen conditions during the MMR in two ways. First, rising oxygen concentrations appear to have permitted the radiation of nutrient-rich planktonic groups that facilitated increasingly efficient food webs and bottom-up transformation of ecosystems. Second, rising oxygen concentrations lifted “top-down” constraints on ecosystems— rising oxygen partial pressures relaxed restrictions on maximum body size and activity levels and allowed for the evolution of the complex predator-prey relationships that form the backdrop of the MMR.

5. CONCLUSION

A step change in atmospheric oxygen concentrations rose to near-modern levels during the Ediacaran is directly linked to the evolution of basal metazoans (Sperling et al., 2013). Here, our data suggests the presence of another "oxygen revolution"—namely during the Mesozoic Marine Revolution. Body size, motility of fauna, and metabolic rates suggest oxygen acted as a pressure limiting body size and activity levels in the Paleozoic and early Mesozoic, acting as a bi-directional pressure on ecosystems through limitations on both large body size and phytoplankton communities. Increasing ocean oxygen concentrations permitted diversification of larger, nutrient rich planktonic groups that could facilitate bottom-up growth of complex ecosystems (Knoll & Follows, 2016a). At the same time, increased coupling of ocean-atmosphere concentrations through ballasting of larger phytoplankton, disappearance of O_2 depleted epicontinental seas, and increasingly open-ocean marine environments led to increasingly ventilated ocean environments for the first time since oxygen concentrations reached modern levels in Earth history (Meyer et al., 2016).

ACKNOWLEDGEMENTS

Chapter three has been prepared for submission to the journal Proceedings of the National Academy of Science and may appear as: Sugla, R. K., Norris, R.D. Increased metabolic demand in the Mesozoic Marine Revolution tracks rising oxygen concentrations. *Proceedings of* the National Academy of Science. (2021). The dissertation author was the primary investigator and author of this paper.

CHAPTER 4

IS THE MODERN DEEP-SEA BIOTA AN ANALOG FOR PALEOZOIC COMMUNITIES?

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ABSTRACT

Over the last 541 Ma, there is a well-documented secular trend in marine invertebrate communities from dominantly sessile or slow-moving taxa in the Paleozoic to more active animals in the Mesozoic. This secular trend in animal activity is seen in animal body size, predation, muscle mass, and bioturbation indices and is hypothesized to reflect a temporal trend in ocean export production and ocean oxygenation. Modern deep-sea communities still bear striking similarities to Paleozoic shallow marine communities. We tested the hypothesis that species with Paleozoic origins survive in the modern deep sea because their physiology, capable of handling reduced pO_2 availability in the Paleozoic, makes them competitively superior to species whose clades and metabolic characteristics evolved in the higher pO_2 world of the Mesozoic and Cenozoic. Using distributional data for modern species, we generate temperature and oxygen state space maps that can be used to infer the critical oxygen partial pressures of each species. When grouped by the timing of clade origin, taxa typical of Paleozoic communities have low-oxygen and low-temperature habitats compared to Mesozoic and younger clades. We suggest that the observed biogeographic shifts of Paleozoic taxa from the shallow marine communities of yesteryear to modern day deep sea communities may reflect their tracking low metabolic rates imposed by low O_2 availability in past shallow marine ecosystems and low temperatures in the modern deep sea.

Mesozoic and Cenozoic taxa, in contrast, are competitively superior in modern shallow marine, high pO_2, high temperature environments, but continue to be at least partly outcompeted by taxa with Paleozoic origins where low temperatures and/or low pO_2 minimize their advantages of highly active physiologies.

1. INTRODUCTION

Deep-sea habitats differ from shallow marine habitats in pronounced ways. In stark contrast to most shallow water and epipelagic systems, deep-sea environments dependent on exported surface marine production are characterized by low production rates (Glover & Smith, 2003; McClain et al., 2012). Hydrothermal vents and cold-seeps are an exception, presumably reflecting the abundant local chemosynthetic production. Carbon flux into the deep-sea is predominantly composed of detritus from surface waters of which only a fraction reaches the ocean floor (Lampitt & Antia, 1997) . At the abyss, for example, deep sea carbon fluxes are less than 5% of production in surface waters (Smith et al., 2009). Furthermore, exported organic detritus may arrive in the deep sea only seasonally, creating a long drought in food supply over the rest of the year (Rice et al., 1986; Turner, 2015). Unlike surface waters, temperatures in the deep sea show relatively little latitudinal and temporal variation. Deep sea ocean temperatures range between -1 to 4°C while sea surface temperature averages vary from 36 °C at low latitudes to as low as -2°C in polar regions.

Physical energy of deep-sea environments is also low compared to shallow marine environments. While benthic environments in deep waters may experience physical disturbances as a result high energy storms, such events are infrequent compared to the wave energy and wind-driven mixing of surface waters (Harris, 2014). Wave action and wind-driven mixing of surface waters maintain surface water oxygen concentrations broadly in equilibrium with the atmosphere. Below the wind-mixed layer, which shoals to tens of meters in the summer and deepens to several hundred meters in the winter, oxygen concentrations vary widely (de Boyer Montégut, 2004; Franks, 2015). Waters underlying highly productive regions such as the Eastern Tropical Pacific have pronounced declines in oxygen concentrations with in the upper 200-300 m of the water column. Such oxygen minimum zones (OMZs) constitute nearly 8% by volume of the entire ocean contains less than 20 umol kg-1 of oxygen (Seibel, 2011). Downwelling in polar regions combined with low rates of oxygen utilization creates well-oxygenated water masses at depths greater than the OMZ (~200-1000m). Deep-sea organisms face additional challenges. Below 200m the availability of photosynthetically active radiation sharply declines, and no light penetrates below 1000 m water depth. Hydrostatic pressure also constitutes additional challenges to life in the deep ocean (Somero, 1992; Wang et al., 2019).

The combination of minimal primary production in most of the deep-sea, limited and highly seasonal nutrient flux from surface waters, low O_2, low temperatures and light availability, and high hydrostatic pressures drive the pronounced changes from shallow to deep-sea habitats (Rogers, 2015). Deep-sea habitats have been shown to be low in biomass, respiration rates, reproduction, recruitment, and bioturbation. Metabolic rates of organisms also decline with increasing depth in the deep-sea, although it remains unclear whether this is primarily due to light availability, chemical energy, or body size and temperature constraints on metabolic rates (A. Brown et al., 2018a; Drazen & Seibel, 2007; Gallo et al., 2020). In contrast, the well-oxygenated and comparatively high primary productivity of surface waters in close proximity to the coast support active ecosystems with high metabolic demands and complex predator-prey relationships. High metabolic rates, community energetics, rates of bioturbation, infaunal and epifaunal tiering, and large body sizes in highly muscled animals are all common in surface waters.

A notable feature of modern deep sea faunas is the abundance of clades whose origins lie in the Paleozoic, raising a perennial question of whether the deep sea is a refugium for clades that long ago died out in shallow marine environments (Figure 6). Species similar to Cambrian fauna such as trilobites (Figure 6b) , inarticulate brachiopods (Stanley, 2020), siliceous sponges (Brunton & Dixon, 1994), and monoplacophoran molluscs can all be found in today's deep ocean (Bush & Bambach, 2011; Sepkoski, 1981). Ordovician or later clades such as stony bryozoans, articulate brachiopods (Figure 6a), stalked crinoids (Figure 6e) (Brett, 1984), and coelocanths (Figure 6g) are all also present (Bretsky, 1969; Droser & Finnegan, 2003; Sepkoski & Sheehan, 1983). Such similarities suggest the possibility that conditions of shallow marine Paleozoic environments and modern deep ocean environments both contain barriers against more active, predatory fauna typical of shallow marine communities in the Mesozoic and later (Buatois et al., 2016a). Identifying the variables which drive similarities between Paleozoic shallow marine communities and their extant deep-sea relatives could provide a mechanistic, physiologically driven explanation of a first-order biogeographic observation in the Earth system and long-term evolutionary trends. Such drivers, however, have never been identified.

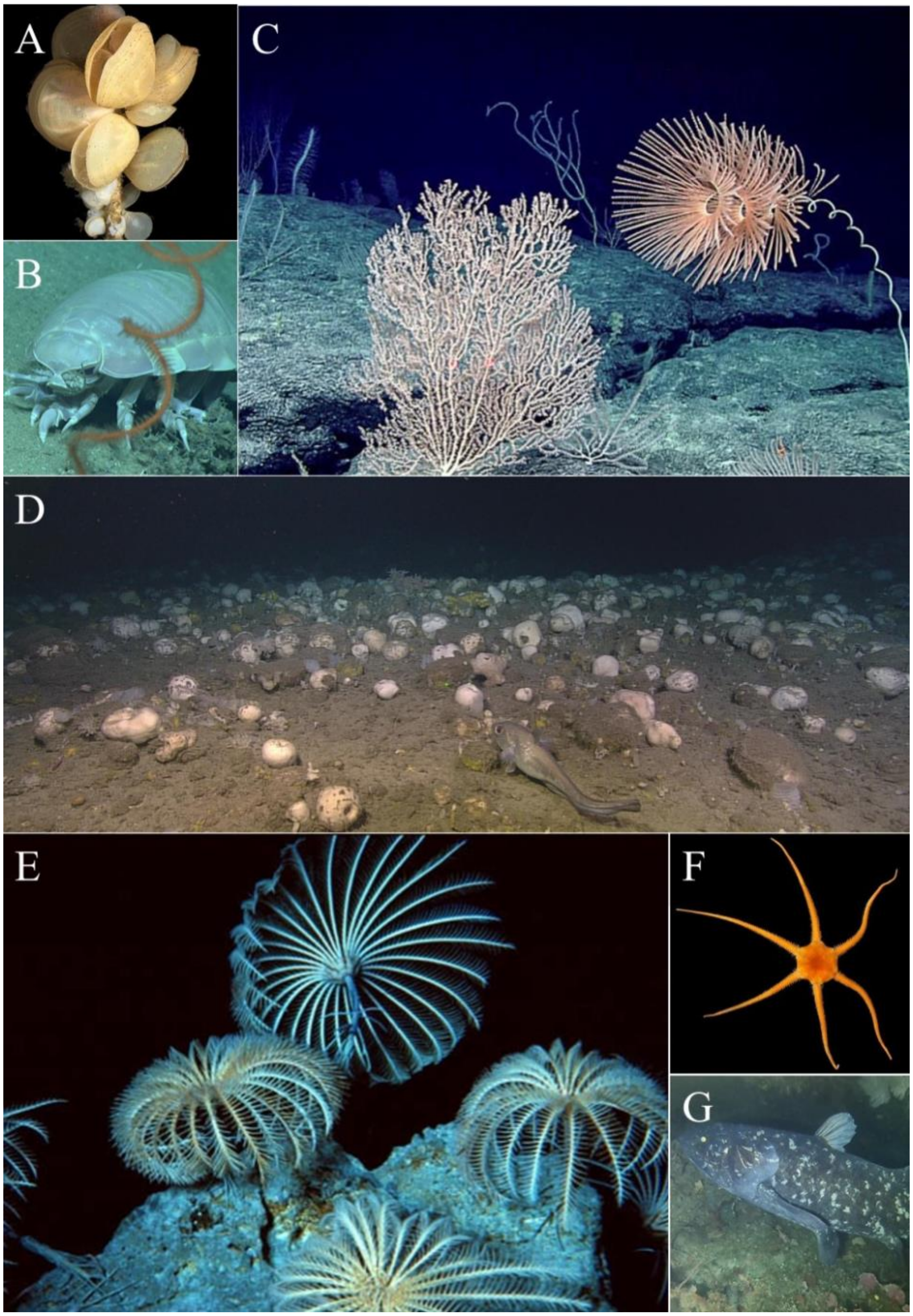


Figure 6 - Examples of Deep-sea organisms with Paleozoic origins. Anecdotal data has often suggested the deep-sea hosts many "living fossil" representatives of ancient clades Much like shallow marine communities of the Paleozoic, these organisms are small, slow-moving, and sessile. Such taxa are common in the deep-sea, despite being less abundant or absent in modern shallow marine environments. A) Liothyrella uva, an articulate brachiopod common to Antarctic waters. B) Deep-sea isopod Bathynomus giganteus. C) Deep water Iridogorgia and bamboo coral in foreground, octocorals in the background. D) Geodia barrette sponge garden in the Flemish Cap. E) Abyssal stalked crinoids. F) Circum-Antarctic brittle star, Ophionotus victoriae G) Living coelacanth seen off Pumala, South Africa.

Here, we explore the possibility that Paleozoic shallow marine communities found refuge in the deep-sea as they were outcompeted in the shallow marine environment during the ‘evolutionary arms race’ of the Mesozoic and Cenozoic. We use data of species distribution to create temperature and oxygen state space maps of modern species. We then group those species into membership in Paleozoic-like and Cenozoic-like communities (hereby referred to as ‘Paleozoic’ and ‘Cenozoic’ taxa) to infer critical oxygen levels for species across a wide range of temperatures. We show that modern Paleozoic-like communities occupy colder, lower oxygenated waters more frequently than species typical of Cenozoic clades and that highly active metabolisms of Cenozoic clades limits them when temperature and oxygen concentrations are low.

2. METHODS

2.1. METABOLIC INDEX DATA

The Metabolic Index has been previously defined as the ratio of O_2 supply to an organism’s resting O_2 demand.

$$\Phi = \frac{\alpha_S}{\alpha_D} B^{\varepsilon} PO_2 \exp\{\frac{E_o}{K_b}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\}$$

Here, α_D is the resting metabolic rate per unit body mass (B) at a reference temperature T_{ref}. α_S is the efficacy of O_2 supply per unit body mass at an ambient oxygen partial pressure PO_2. At the lowest oxygen partial pressure (p_{crit}) that can sustain resting metabolism (where $\Phi = 1$), resting vulnerability of hypoxia (V_h) can be defined as $V_h = \frac{\alpha_S}{\alpha_D}$. We use the inverse of resting vulnerability of hypoxia as measure of resting hypoxia tolerance (A_o), defined as $A_o = \frac{1}{V_h}$. A second metabolic trait utilized here is the sensitivity of hypoxia vulnerability to temperature E_o. As previously defined, $E_o$is equal to the difference between the temperature variation of resting metabolic rate and O_2 supply and can be described by the exponential Arrhenius function. $K_b$is equal to the Boltzmann constant and ε is the allometric scaling of O_2 supply-to-demand ratio.

The state-space habitats of each species were constructed by pairing their location data with hydrographic conditions at those locations (See **Error! Reference source not found.** in Appendix C). Species for each group were selected based on origination times for each organism (i.e. clade origination in the Paleozoic, Mesozoic, or Cenozoic). (See Table 2 in Appendix C). Data with fewer that twenty occurrences were rejected from the study. Occurrence data were downloaded from the Ocean Biogeographic Information System (OBIS; http://obis.org) in Jan. 2021. To estimate the hydrographic conditions at each specimen location, we used monthly climatological temperature and oxygen fields at a 1^{o} latitude and longitude resolution and at 33 depths from the World Ocean Atlas. Hydrographic conditions were determined at the central depth of the minimum and maximum depths reported by OBIS, or from either depth alone if only one metric was provided. Occurrences were discarded if the range of conditions within that depth range differed from the central estimate by more than $2^{o}C$ for temperature or 20% for O_2. For occurrences lacking depth information altogether, we assigned a minimum depth at the sea surface and maximum depth at the seafloor. In cases where even this maximum uncertainty in depths satisfied the error tolerance ($2^{o}C$ for temperature and 20% for O_2) the location data was retained. Metabolic index data was fit to species distribution data following previously described methods. Metabolic index curves indicating increasing hypoxia tolerance with temperature were rejected, as this would imply infinite hypoxia tolerance with increasing temperatures.

A composite state-space habitat for Mesozoic and Paleozoic species was constructed as a weighted average of an occurrence metric across all species in each group. Two occurrence metrics were used. The first was a simple binary presence/absence, for a given species i, denoted

H_i^{PA} (for 'Habitat Presence/Absence'). If any reported location of the species maps to climatological data in a given temperature/pO$_2$ bin, then that species is considered to inhabitat that type of environment, and it contributes to the overall occurrence of that taxonomic group (Mesozoic or Paleozoic) to habitat conditions of that T/pO$_2$ range. The second metric is a relative occurrence, denoted H_i^{FO} (for 'Habitat Fractional Occurrence'), which sums all occurrences in each T/pO$_2$ bin, and divides by the total number of species sightings. For example, if 90% of all reported sightings are in regions of the ocean where temperature is between 10-11^{o}C and pO$_2$ is between 20-21 kPa, then the state-space diagram for that species would be 0.9 in that T/pO$_2$ grid cell. For a given species (indexed by i) the sum of H_i^{FO} across all of T/pO$_2$ state-space is 1.

To average these metrics across all species within each group, we computed the weighted sum of each metric (H_{PA} or H_{FO}) for each T/pO2 bin, where the weights are determined by the total number of species observations (See Figure 14 in Appendix C). For example, the state-space habitat of Mesozoic species using the presence/absence metric would be:

$$H_{Meso}^{PA} = \frac{\sum_{i=1}^{N} H_i^{PA} * w_i}{\sum_{i=1}^{N} w_i}$$

Where N is the number of species in each paleo group (N=52 for Mesozoic, and N=28 for Paleozoic). This weighting is designed to ensure that species with few reported occurrences that only partially sample its true state-space habitat, do not weigh as heavily as those with large databases, in computing the overall state-space habitat. However, we also do not want the weighting to be heavily skewed toward any species with enormous number of observations. A convenient weighting that strikes this balance is a simple saturating function (Figure 14):

$$w_i = \frac{n_i}{n_i + K_n}$$

where n_i is the number of individual observations for species i in OBIS that can be matched to hydrographic conditions satisfying the quality control criteria outlined above. We find that the state-space habitat diagrams are very similar across a wide range of weighting factors (Kn from 10 to 1000), indicating that the depiction of Paleosoic and Mesozoic taxonomic niches are highly robust.

2.2. PALEOGRAPHIC RECONSTRUCTIONS

Plate reconstructions were completed using occurrence data from the Paleobiological Database (PBDB) and Digital Elevation Models of Phanerozoic paleogeography from the PALEOMAP PaleoAtlas project. Data from the Paleobiological Database was prepared by subsetting all occurrence data to include only marine clades. Data from freshwater depositional environments were excluded based on designations in the PBDB. As an additional check, analysis was limited to fossil specimens identified at the species and genus levels. Occurrence data was then binned into a ten million year timescales and data within +/- five million years of the desired time intervals for paleogeographic reconstruction (450 Ma, 300 Ma, and 150 Ma) were used. Latitude and longitude for fossil specimens were then rotated to the correct paleocoordinates using the chronosphere package in R and data from the PALEOMAP PaleoAtlas project.

3. RESULTS

Species distribution data from OBIS were collected and aggregated into groups representative of Mesozoic and Paleozoic fauna. Distribution data was utilized to construct inferred metabolic index curves for each taxon. The inferred metabolic index curves are plotted in temperature and oxygen state space. The aggregated metabolic index curves indicate differences between the two communities. Frequency distributions of hypoxia tolerance (Ao) at the reference temperature of 15°C shows different distributions for each group. Mesozoic fauna show a right skewed distribution of Ao towards lower higher critical oxygen tensions. Paleozoic fauna show a flat frequency distribution, approaching an uniform distribution of hypoxia tolerance at the 15°C reference temperature. Frequency distributions for temperature sensitivity of hypoxia tolerance (Eo) are similar for both groups. The distributions for both Paleozoic and Mesoozic fauna show a peak in Eo centered around a mean of ~0.15 and a decrease in frequency above and below this point.

Distribution data in OBIS aggregated into temperature and oxygen state space with weighted presence/absence and weighted frequency of occurrence show different patterns for each group. While overlap exists between both groups, there are substantial differences between them as well. Broadly, temperature and pO_2 distributions for of modern taxa with Paleozoic origins show an affinity towards low temperatures and oxygen partial pressures compared to taxa of Mesozoic origin. For Mesozoic fauna, the inferred metabolic index curves show an affinity towards temperatures above 17°C and oxygen partial pressures above 25 kPa. Paleozoic fauna have metabolic index curves that indicate a preference for moderate and low temperature environments below 20°C. At temperatures below 20°C Paleozoic organisms are able to tolerate oxygen pressures greater than 10 kPa. At temperatures lower than 10°C, Paleozoic taxa seem able to tolerate O_2 partial pressures above 15 kPa. These plots indicate Mesozoic taxa and Paleozoic taxa occupy different temperature and oxygen partial pressure state spaces despite broad overlap at some T/pO_2 regimes.

3.1. PALEOBIOLOGICAL OCCURRENCE DATA

Occurrence data of marine fauna obtained from the Paleobiology Database and projected onto paleographic reconstructions (Figure 7) show Paleozoic assemblages (at 450 Ma and 350 Ma) on shallow shelfs or in epicontinental sea environments. Occurrence data at 150 Ma show tectonic rifting leading to marine communities increasingly found in open ocean environments in the Late Mesozoic and Cenozoic.

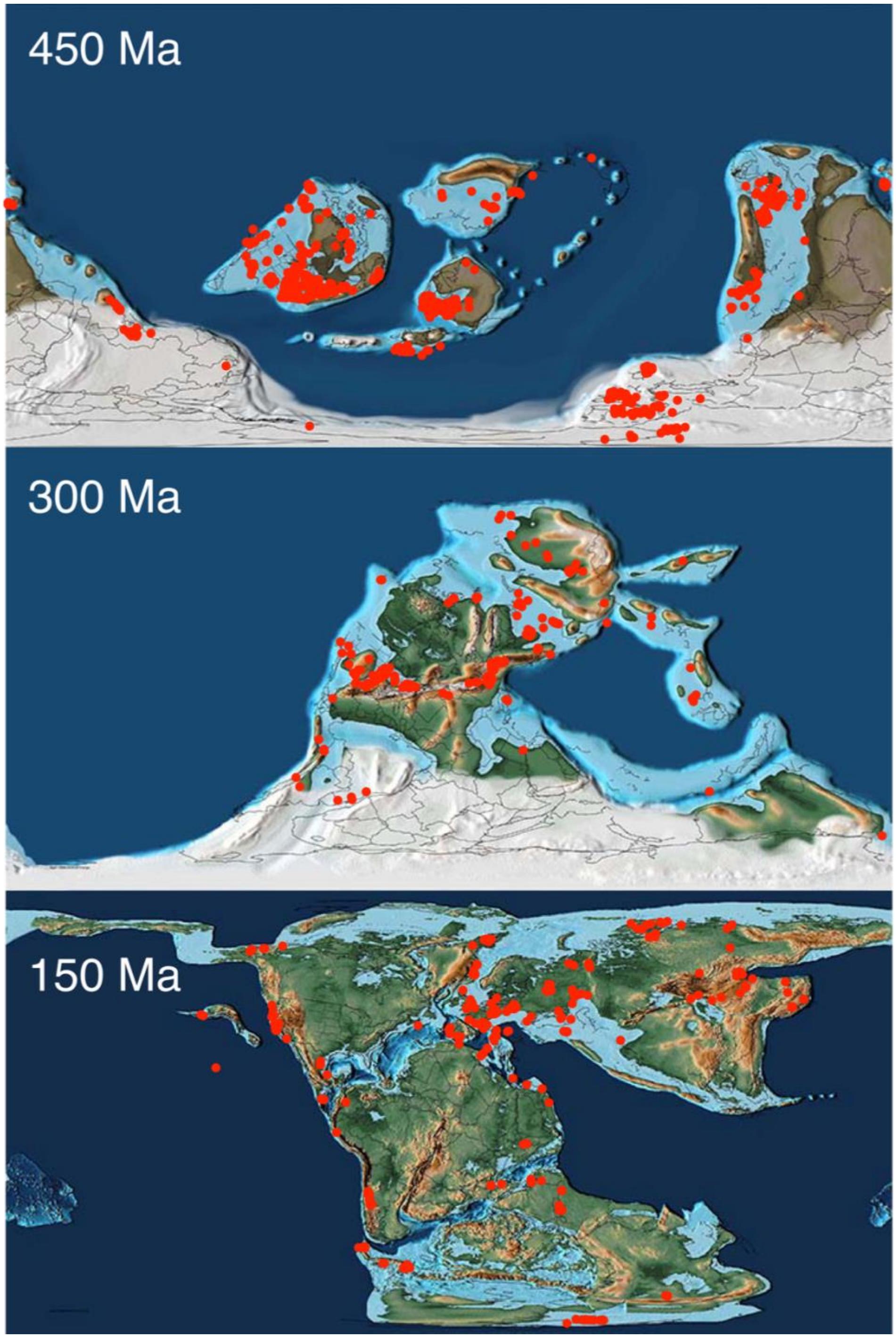


Figure 7 - Occurrence data for marine fauna through time. Top row shows occurrence data for marine fauna at 450 Ma, second row at 300 Ma, and bottom row at 150 Ma. Paleogeographic reconstructions show rifting led to increasing open-ocean and well-ventilated environments.

4. DISCUSSION

Deep-sea ecosystems compositional similarities to shallow marine communities of the Paleozoic, yet the reasons for these similarities are poorly understood. Paleozoic fossil assemblages were rich in sessile animals with low degrees of infaunal tiering and relatively simple predator-prey relationships (Allmon & Martin, 2014b; Buatois et al., 2016b; Dunne et al., 2008; Huntley & Kowalewski, 2007; Vermeij, 1983; Vermeij, 1977b). Extant relatives of early Phanerozoic communities, such as stalked crinoids, monoplocaphoran molluscs, and inarticulate brachiopods, are abundant in the deep-sea today (Figure 6) (Ameziane & Roux, 1997; Eléaume et al., 2012; Sigwart et al., 2019; Zezina, 1994). Data presented here suggests similarities between modern deep-sea communities and Paleozoic shallow marine communities may be the result of physiological limitations of more active taxa with Mesozoic and Cenozoic origins, particularly in cold, poorly oxygenated waters.

When hypoxia tolerance (Ao in Figure 8b) is plotted, Mesozoic taxa show skewness towards higher *resting* hypoxia tolerances when plotted as frequency distributions (Figure 8b). Taxa with Paleozoic origins instead show near uniform frequency distributions of critical oxygen partial pressures when at rest at a common reference temperature. These hypoxia tolerances are identical to resting critical oxygen partial pressures (pcrit) at a reference temperature of 15°C. The differences in these distributions suggest that extant taxa with Paleozoic origins may better suited to low oxygen environments than modern counterparts even when not engaging in high activity behaviors.

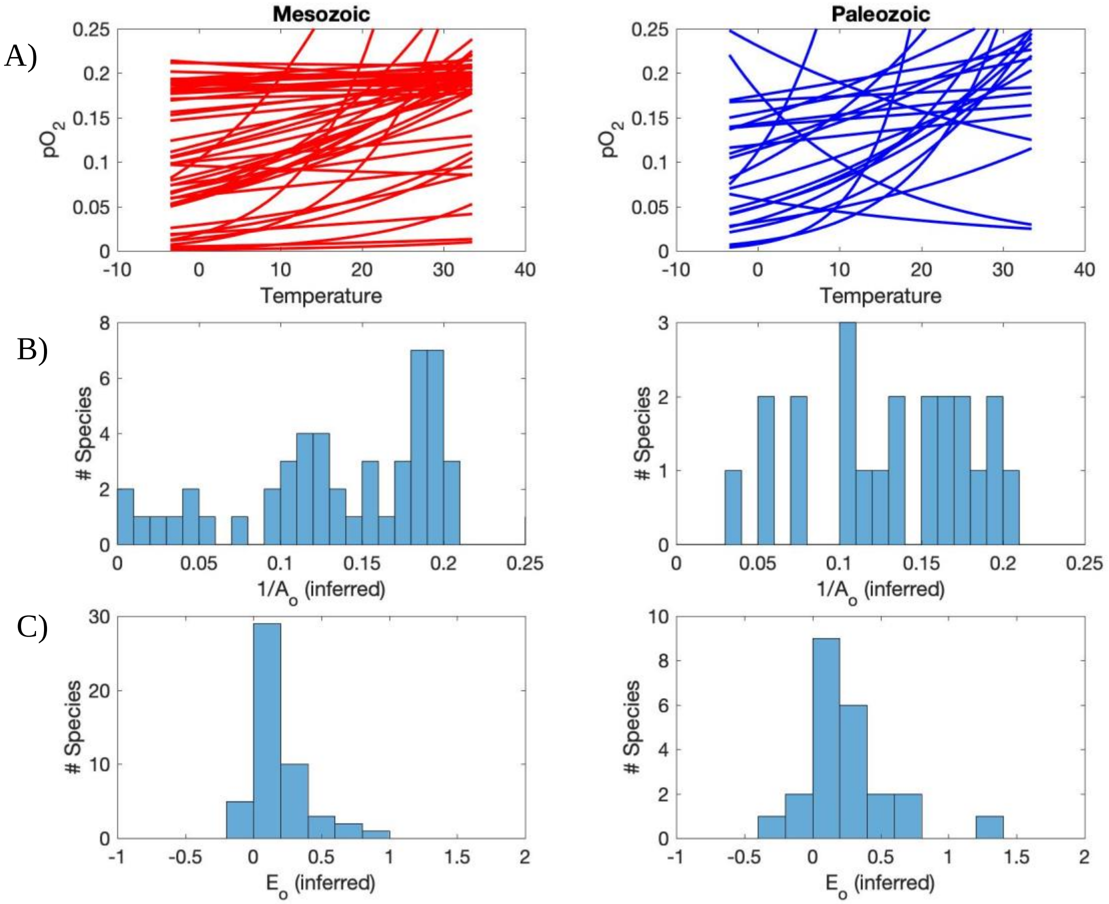


Figure 8 - Metabolic index curves and metabolic traits for Mesozoic and Paleozoic taxa. Top row shows inferred metabolic curves estimated from distributional data in the Ocean Biodiversity Information System (OBIS) in temperature/pO2 state space. Second row shows frequency distribution of hypoxia tolerance (Ao) in both groups. Third row shows temperature sensitivity of hypoxia tolerance in both groups (Eo). Metabolic index and metabolic trait data suggests that at low-to-intermediate temperatures Paleozoic fauna have greater hypoxia tolerance. Temperature sensitivity of hypoxia vulnerability shows no significant difference between both groups.

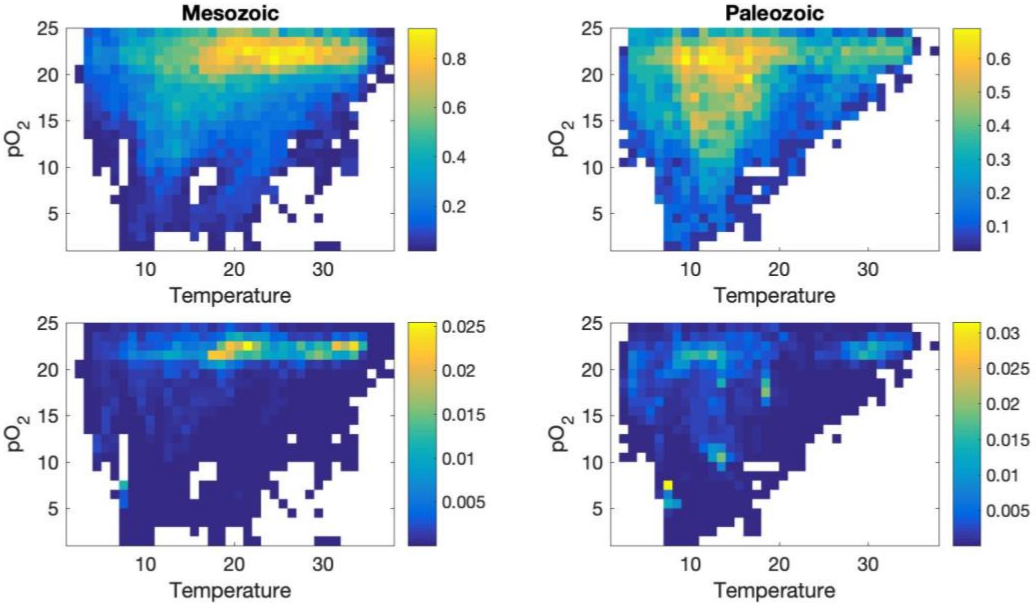
The temperature and oxygen state space curves calculated from modern species distribution data (OBIS www.obis.org) also suggest distinct differences in oxygen tolerance in Paleozoic and Mesozoic taxa (Figure 8a). The standard Metabolic Index used to generate the curves in Fig. 2a reflects the aerobic energy balance of an organism and is defined by the ratio of oxygen supply to oxygen demand. In order to maintain resting metabolism the physiological oxygen supply must exactly meet resting oxygen demand (where the metabolic index is equal to 1).

Resting metabolic rates, however, do not take into account additional energetic demands for an organism to engage in critical activities such as hunting, migration, foraging, mating, or reproduction (Deutsch et al., 2020). Such activities require additional aerobic energy between that of resting and maximum metabolic rates. We refer to this metabolic rate as the sustained metabolic rates and the minimum Metabolic Index required to support sustained metabolic rates as the critical Metabolic Index. As previous studies have shown, the temperature and oxygen state-space curve calculated from species distribution data, such as those shown in Figure 8a, follow the boundaries of an organism's *critical* Metabolic Index curve.

The critical metabolic index data suggest that hypoxia tolerance of Mesozoic communities engaging in essential ecological activities is reduced across a wide range of temperatures relative to taxa with Paleozoic origins or Paleozoic analogs. While both Paleozoic and Mesozoic groups show wide variance in inferred pO_2 and temperature range, modern groups show a distinct skew towards less hypoxia tolerance at low and intermediate temperatures. Paleozoic species, in contrast, appear particularly tolerant to hypoxia at cold temperatures. At high temperatures, it appears both groups gravitate toward high pO_2 environments and away from hypoxic conditions.

Importantly, when temperature sensitivity of hypoxia tolerance (Eo) is plotted, both Paleozoic species and Mesozoic species have similar distributions (Figure 8c). The temperature sensitivity of hypoxia tolerance reflects both oxygen demand and an organism's ability to modulate oxygen supply. Changes in Eo between species may reflect differences in life history and ecologies of individual species, rather than traits that may be phylogenetically conserved. The similarities in Eo between Paleozoic-like species and Mesozoic-like species suggests that differences in hypoxia tolerance likely reflect evolution, rather than being the byproduct of differing sensitivities to environmental temperature throughout an organism's life cycle.

Temperature and oxygen state space aggregated and plotted with presence and absence data for Paleozoic and Mesozoic taxa supports the hypothesis that the evolution of Mesozoic and later clades were limited by oxygen (Figure 9).



Top row:
Presence
vs Absence
(Weighted)

Bottom row:
Frequency of
Occurrence
(Weighted)

Figure 9 – Aggregated and weighted temperature (degrees centigrade) and pO_2 (kPa) state-space for Mesozoic and Paleozoic groups. Top row shows weighted presence/absence data for fauna and a clear preference for Paleozoic fauna in cold/low pO_2 waters. Bottom row shows frequency of occurrence data for Paleozoic and Mesozoic groups.

When weighted for number of observations, Mesozoic fauna show a clear trend towards presence in warm, well oxygenated waters with pO2 above 20-25 kPa and temperatures generally above 17-18°C. Below this range, presence of Mesozoic taxa drops markedly indicating these clades operate in a relatively narrow range of high temperature and oxygen conditions. In comparison, Paleozoic taxa show a trend towards cold water temperatures below 20°C and a wider minimum pO2 range, between 10-25 kPa. While Paleozoic taxa skew towards colder temperatures their inferred Metabolic Index shows that they are able to survive at higher temperatures as well, comparable to many Mesozoic taxa. The cold temperatures and often low pO2 of the deep-sea present physiological challenges for Mesozoic taxa with high metabolic rates compared to living Paleozoic taxa.

These results suggest that temperature dependent hypoxia tolerance may play a critical role in the biogeographic changes in shallow marine communities between the Paleozoic and today. At a wide range of temperatures, Mesozoic fauna appear have reduced tolerance to hypoxia than Paleozoic taxa. At high temperatures, both Mesozoic and Paleozoic taxa have broadly similar tolerances for hypoxia and are able to sustain their physiological demands. Both groups os species appear to have a limited physiological range under high T, high pO_2 conditions, likely because O_2 quickly imposes severe limitations on organisms whose metabolisms are already working hard due to the high environmental temperature. At high temperatures and low oxygen conditions, neither group is able to sustain metabolic demands. However, on the low end of the temperature scale, Paleozoic taxa thrive even when oxygen partial pressures are low. One potential explanation for this is that at high temperatures aerobic scope becomes reduced as basal metabolic rates increase with temperatures, while maximal metabolic rates cannot exceed that of atmospheric partial pressures. Organisms that with active physiologies across a wide range of body sizes, like many

Mesozoic taxa, may be unable to engage in activities necessary for survival, particularly when oxygen conditions are low. Active Mesozoic taxa may be limited through both low temperature and low oxygen supply which together depress the functional activity level of these species. Cold temperatures may impose a variety of roadblocks against oxygen supply in organisms, such as slower diffusion across the gill-water membrane, for example. Research on the effects of low temperature on oxygen supply is still limited, however, and more is needed to assess whether this is the driver of the trends outlined here. In addition, one limitation of this dataset is that many of the species used as extant relatives of Paleozoic communities are from deep-sea environments. As a result, they experience a narrow range of temperatures across the duration of their lifecycle. Such a narrow temperature range may mean oxygen thresholds at the high temperatures are inaccurately assessed.

4.1. IMPLICATIONS

The fossil record from Paleozoic communities are overwhelmingly from tropical epeiric seaways (Figure 7). Paleotemperature reconstructions suggests epeiric seas in the Paleozoic may have experienced temperatures in excess of 40°C, substantively higher than temperatures experienced in the modern ocean today (Goldberg et al., 2021). Even at high latitudes (~65 to 70 degrees South), temperatures reached an average of ~20-25°C (Hearing et al., 2018). In addition to high temperatures, models and geochemical data of oxygen partial pressures suggest poorly and irregularly oxygenated oceans throughout the Paleozoic (Dahl et al., 2010b; W. Lu et al., 2018; Martin & Servais, 2020; Van De Velde et al., 2018). Warm epeiric seas of the Paleozoic regularly experienced hypoxic events due to restricted flow into continental seaways, coastal salinity stratification of the water column, and high nutrient input from nearby coastal areas.

Low oxygen partial pressures in the water column and high temperatures during Paleozoic hothouse environments should reduce hypoxia tolerance in aquatic organisms. Reduced oxygen partial pressures reduce organismal oxygen supply, while warm ocean temperatures raise resting metabolic rates. Combined, these changes result in reduced aerobic scope (the difference between maximal and resting metabolic rates at a particular temperature) (Deutsch, 2015; Rubalcaba et al., 2020; Seibel & Deutsch, 2020). Consequentially, if Paleozoic seas were more hypoxic than they are today, as suggested by diverse modeling and marine geochemistry, the combination of warm seas and extensive ocean hypoxia may have been a barrier in the radiation of the active fauna prior to the Mesozoic Marine Revolution (R. a. Berner et al., 2005; Van De Velde et al., 2018).

Over the course of the Phanerozoic, tectonic reconfigurations and changing climatic conditions drastically changed the marine landscape. The epicontinental seaways recorded in most the fossil record dried up as tectonic rifting split up Pangea. Narrow shelves that are harder to drive into hypoxia, rising ocean oxygen partial pressures, well-ventilated mixed oceans, Cenozoic cooling, and radiations of primary producers gradually relaxed pressures that selected for low metabolic activity fauna in shallow marine environments (Allison & Wells, 2006; Allmon & Martin, 2014; Knoll & Follows, 2016; Korte et al., 2015; Smith & Thatje, 2012). We suggest that better oxygenation of warm coastal waters increased the overall aerobic scope of shallow marine biotas, enabling the evolution of metabolically active Mesozoic clades. Indeed, occurrence data show that the fossil record from Mesozoic and later fauna were increasingly found in such open ocean environments (Figure 7). Some Paleozoic taxa also took advantage of this increased metabolic scope, but many found that the physiologies that worked so well in the warm, hypoxic epicontinental seas were now placed at competitive disadvantage in shallow marine ecosystems.

By comparison, deep ocean environments impose limitations on metabolically active fauna that may have restricted the invasion of Mesozoic taxa into deeper ocean environments. These conditions may have provided refuge for Paleozoic-like communities that once occupied shallow marine environments. The modern deep-sea, unlike the shallow seaways of the Paleozoic, is usually well-oxygenated but presents other physiological barriers for active fauna. Low temperatures characteristic of the deep ocean may result in a decrease in metabolic rates due to the well-documented temperature effects on metabolic rates described by Q10 and the metabolic theory of ecology (McClain et al., 2012). Hydrostatic pressure also exerts an energetic cost (A. Brown et al., 2018b; Somero, 1992). Previous studies show that some deep-sea fish have adaptations on the cellular to physiological levels to adapt to the high pressure of the deep-sea. Reduced food/energy availability likely constitute additional barriers against high metabolic activity and diversity in the deep sea (Levin & Gage, 1998; Kenneth L. Smith et al., 2018).

Some studies suggest that selection pressures for high metabolism relax with depth in taxa reliant on visual information gathering for predation (BA Seibel, 2007). Another possibility, then, is that visual predators that become common in the shallow marine environments in the Mesozoic have no reason to maintain a high metabolism in the deep-sea due to limited light availability. Indeed, many deep-sea organisms that do not rely on visual systems as the primary source of sensory information intake appear to have similar metabolic rates at most ocean depths. Given that the Mesozoic Marine Revolution is characterized by an increase in predation and a reliance of visual environmental intake, we expect this may be another barrier towards metabolically active fauna in the deep sea.

5. CONCLUSION

There are substantial physiological and ecological barriers for Mesozoic species in the deep sea. Our data suggests that Paleozoic species exhibit tolerance to a wide range of oxygen partial pressures across moderate to low temperatures when compared to Mesozoic taxa, which may partially explain the continued presence of Paleozoic taxa in the deep-sea. Mesozoic and Paleozoic taxa appear to have statistically different critical oxygen thresholds at intermediate temperatures of 15°C and that this difference may be phylogenetically driven.

A common suggested driver for the Mesozoic Marine Revolution is radiation of large, nutrient dense phytoplankton communities increasing the availability of nutritional resources. Our data also suggest that oxygen imposes strong constraints on Mesozoic taxa relative to Paleozoic taxa at most temperatures, and that the oxygen and temperature may be have been limiting variables towards more active fauna in shallow marine environments across Phanerozoic time.

As these physiological constraints relaxed with increasing oxygen availability, Mesozoic and Cenozoic fauna began to expand in shallow marine environments, while the environmental conditions in the deep-sea created refugia for Paleozoic taxa that once were common in shallow marine environments but were gradually outcompeted. The data here also suggest that over much of the Phanerozoic, deep-sea and shallow marine environments experienced distinctly different oxygen partial pressures, similar to modern ocean. We suggest such differences played an important role in the long-term evolutionary trends of life in the ocean, and provide an evolutionary foundation for the biogeographic trends between shallow marine and deep sea ecosystems.

ACKNOWLEDGEMENTS

Chapter four has been prepared for submission to the journal Science and may appear as: Sugla, R. K., Deutsch, C.A., and Norris, R.D. Is the modern deep sea biota an analog for

Paleozoic communities? Science. (2021). The dissertation author was the primary investigator and author of this paper.

CHAPTER 5

CONCLUSIONS

1. MAJOR FINDINGS

Canonical models of atmospheric oxygen have long suggested an early rise in atmospheric oxygen in the Neoproterozoic followed by a subsequent maximum in pO2 in the Carboniferous produced by widespread coal deposition (Lyons et al., 2014; Scott & Glasspool, 2006; Wallace et al., 2017). Outside of these events, model estimates of atmospheric oxygen for the Phanerozoic show little overlap with one another (Mills et al., 2016). Despite the many suggested links between oxygen partial pressures and the evolution of life, such models also show little correlation to the evolutionary trends in marine fossil record (Bambach, 1993; Berner et al., 2005; Droser & Bottjer, 1989; Heim et al., 2015; Thayer, 1979). This dissertation reframes the scientific outlook of oxygen and evolution across Phanerozoic time through the development of novel sedimentary proxies and analysis of the physiological activity of modern fauna representative of ancient clades. The end result of this dissertation is a view of Phanerozoic oxygenation that better distinguishes the dynamics of atmospheric oxygen from oceanic oxygenation, which appear to have been distinctly different even over multi-million year timescales. An additional major contribution of this thesis is assessing oceanic oxygenation and its relationship to major biological trends towards increasing energetics, burrowing, tiering, and body size evident in the marine fossil record. The research presented in this thesis is among the first to reconstruct trends in benthic oceanic oxygen across the Phanerozic and contextualize these dynamics through a paleobiological lens. The end result is a view of biological evolution and oxygen in the marine environment that are broadly consistent with one another.

The first chapter of this thesis addresses a longstanding observation in sedimentary geology. In the 1970s sedimentologist Derek Ager commented on the ‘persistence of facies’ (Ager, 1973). Notably, carbonate sediments in outcrops across the globe held to a remarkable pattern---the geologic age of sediments could broadly be determined by their color. Carbonates of Mesozoic and Paleozoic age were darker in color, often black and grey, while Cenozoic sediments were light colors such as white and tan. While Derek Ager never explained the drivers of this pattern nor quantified it, his observations pointed to a first order, seemingly global observation that demanded explanation.

My thesis directly addresses this by quantifying the reflectance spectra from a global sample of carbonate sediments. I find that there is an abrupt shift in the colors of carbonate rocks at ~200 Ma from nearly uniformly grey carbonates in the Paleozoic and early Mesozoic, to predominately white, yellow or tan carbonates in sequences younger than ~100 Ma. I show that this abrupt shift in sediment color occurs across depositional environments—from intertidal to deep sea sediments. As sediment color is largely driven by the presence of organic matter and redox sensitive trace metals in sediments, I posit that sediment color tracks oxygenation at the sediment water interface. Indeed, the data strongly suggests changing oxygenation patterns in ocean basins in the Late Mesozoic and Cenozoic. By ~ 100 Ma carbonate sedimentary facies are persistently oxic. This result seems to directly contradict models of atmospheric oxygen which suggest pO_2 reached at Phanerozoic maxima in the Carboniferous. However, an alternative is that while atmospheric oxygen may have climbed to near modern or even higher pO2 by the Carboniferous, the ocean floor was evidently substantially hypoxic until the early Mesozoic. By examining the paleogeographical distribution of my samples, I suggest that despite a potential Carboniferous atmosphere hyperoxic relative to today, the unique environmental conditions of epeiric seas prevalent throughout much of the Paleozoic may have led to long-term decoupling between oceanic and atmospheric oxygen concentrations.

My second chapter shows that the metabolic demand of marine communities in the Phanerozoic mirrors increases in ocean oxygen concentrations suggested by the sediment color record in Chapter 1. It is well known that the “Mesozoic Marine Revolution” (MMR) produced clades that were increasingly efficient at burrowing, practicing effective predation, or defense, and increasing both body size and muscle mass compared to Paleozoic taxa (Bambach, 1993; Bottjer & Ausich, 1986; Knoll & Follows, 2016a; Oji et al., 2003; Smith et al., 2016; Van De Velde et al., 2018). Mass specified metabolic rates normalized to the same temperature indicate that the MMR is not due to increased physiological efficiency of organisms per unit mass, since marine organisms, as a whole, show no overall trend in mass specific metabolic rates. These data suggest that there has not been an overall increase in mass specific metabolic rates as might reflect an overall evolutionary drift toward faster or more efficient metabolisms. Instead, increases in body size lead to higher metabolic demands in agreement with the Metabolic Theory of Ecology (Brown et al., 2004b). Since organisms with large body sizes and high activity levels may be less tolerant of low oxygen partial pressures, we suggest that this result supports the hypothesis that low oxygen concentrations were a limiting variable impeding the evolution of increasingly active marine communities in the Phanerozoic (Rubalcaba, Verberk, Hendriks, et al., 2020). This result departs from the current scientific paradigm which suggests the Mesozoic Marine Revolution was exclusively driven by increase in food availability as larger primary producers radiated in coastal and subsequently pelagic environments (Knoll & Follows, 2016a).

My third chapter examines similarities in community composition between modern deep-sea and Paleozoic shallow marine ecosystems in light of the evidence produced in the first two chapters. The modern deep sea is full of taxonomic groups or look-alike clades that harken to the Paleozoic. These include stalked crinoids, coelacanths, glass sponges, stony bryozoans, articulate brachiopods, solitary cup corals, and even trilobite-like isopods (Amemiya et al., 2013; Chamberlain et al., 1986; Eléaume et al., 2012; Leys et al., 2004; Sigwart et al., 2019; Zezina, 1994). Are these taxa really living fossils, reflective of having lost a competitive edge with more active, more metabolically efficient shallow marine taxa? If rising oxygen concentrations drove shallow marine animals towards increased size and activity during the Mesozoic Marine Revolution, we might expect that the similarities of modern deep-sea communities to Paleozoic shallow marine communities reflect oxygen availability. Using modern distributional data of fauna projected onto temperature/pO_2 state space, I show that extant relatives of Paleozoic clades in the deep-sea operate in temperature and oxygen state spaces incompatible with the high metabolism of shallow marine organisms that originated in the Mesozoic and later. This result is consistent with the hypothesis that the Paleozoic-like" modern deep sea biota persists because there organisms win the selective competition for being able to operate in an environment where both low O_2 and low environmental temperatures limit the levels of metabolic activity that can typically be achieved. In contrast, modern shallow marine organisms work efficiently in warm, well oxygenated environments where they can effectively outcompete most of the Paleozoic holdovers and their modern functional analogs. This chapter provides the first mechanistic explanation based on the physiology of fauna for the similarities between Paleozoic shallow marine and modern deep-sea organisms.

2. FUTURE RESEARCH

The research presented here yields a number of potential future research opportunities. The relationship between sediment color and sediment geochemistry warrants further exploration.

While preliminary results using X-Ray fluorescence tentatively supports the link between redox sensitive trace metals and sediment color, further refinement of this relationship using techniques to estimate highly reactive iron, examination of pyrite framboids under scanning electron microscope, organic matter measurements, and more detailed X-Ray fluorescence measurements would be useful to build quantitative linkages between sediment color and sediment geochemistry. An additional line of research would focus on in-situ studies of modern sediment chemistry and color that include measurements of bottom water oxygen, pore water oxygen levels, pore water chemistry, and porosity of sediments. This research could potentially yield more quantitative usage of sediment color as a proxy for past benthic oxygen concentrations.

This dissertation also suggests oxygen concentrations are a limiting variable towards larger body size and/or increased metabolic activity over long geologic timescales. Given the current debate surrounding marine oxygen partial pressures and body size, this research suggests further examination of these linkages. The maximum metabolic rates of modern organisms are physiologically tuned to the highest oxygen partial pressure experienced by an organism during its life cycle, usually atmospheric pO_2 for shallow marine organisms. Future research examining the overall effects of atmospheric pO_2 lower than today's on body size and energetics of marine communities would be useful for interpreting the trends present in the marine fossil record. This work could also focus on the impacts of highly stratified water columns with minimal hydrographic connection to open environments, such as in Paleozoic epeiric seas, or on water column oxygen concentrations decoupled from atmospheric pO_2 below wind-mixed surface waters.

Research focusing on community composition and energetics as a function of changing oxygen concentrations would also inform a better understanding of the past. In particular, careful examination of how shifts in marine oxygen partial pressures affect the structure of benthic communities would help inform our understanding of the fossil record. While much research has been done in oxygen minimum zones of Eastern Boundary Currents and it's affect on marine community structure, these environments have rapid declines in oxygen concentrations with depth. Such steep declines in depth towards extremely low oxygen partial pressures make them less than ideal natural laboratories for understanding how oxygen concentrations at moderate to low concentrations affect community structure.

Another line of research of personal interest is the long term evolution of information exchange in marine environments. While much research has been done on how individual organisms intake and incorporate information from there environment, a promising line of research in the opinion of the author is examining information transfer between organisms of the same species, organisms of different species, and the physical environment. Such information transfer can be quantified in the unit of bits and has the potential to open up new and interesting lines of research. Bits of information are a unit of measurement readily transferrable across different scales and between the living and non-living environment. Little research has been done of the magnitude of information transfer happening at an ecosystem scale, and I believe this will be an important line of research going forward in the future. Preliminary research not presented here suggests that information may scale with an organism's body size and that the type of sensory systems relied on by organisms may be bounded by physical constraints. If so, this preliminary research suggests there are underlying principles governing the types of sensory systems used by an organisms and the magnitude of information an organism can intake. I suggest exploring the links between size, sensing, and information intake. Developing a firmer understanding of this nexus may potentially yield the ability to understand information exchange over long evolutionary timescales. I also propose that such findings would be of interest to the dynamics of evolution over time. The links between sensory experience, behavioral plasticity, and evolution would greatly benefit from such research.

3. FINAL SUMMARY

Understanding the dynamics of atmospheric and oceanic oxygen concentrations is fundamental to our understanding almost every major process on the planet, including the evolution of life. This thesis builds upon decades of research analyzing the history of oxygen on our planet over the last 2.5 Ga and it's relationship to macroevolutionary trends of multicellular life in the fossil record. I focus on the Phanerozoic, an interval which began with the radiation of representatives of all modern metazoans. This thesis contributes to this existing body of knowledge by constructing one of the first Phanerozoic records of relative oxygen concentrations in benthic environments, showing the importance of examining how oceanic and atmospheric oxygen concentrations can be decoupled over intervals of geologic time, and providing powerful physiological explanations for some of most pronounced trends in the marine fossil record.

APPENDIX A

SUPPLEMENTAL MATERIALS FOR CHAPTER 2

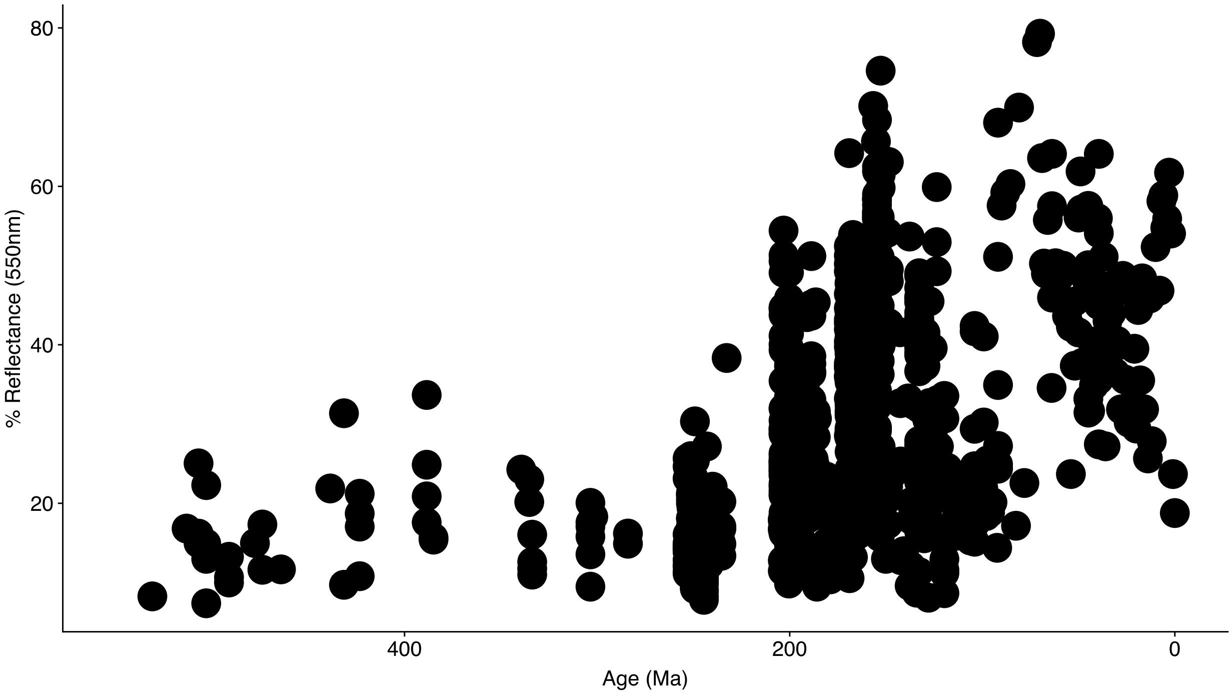


Figure 10 – Reflectance data at 550nm.

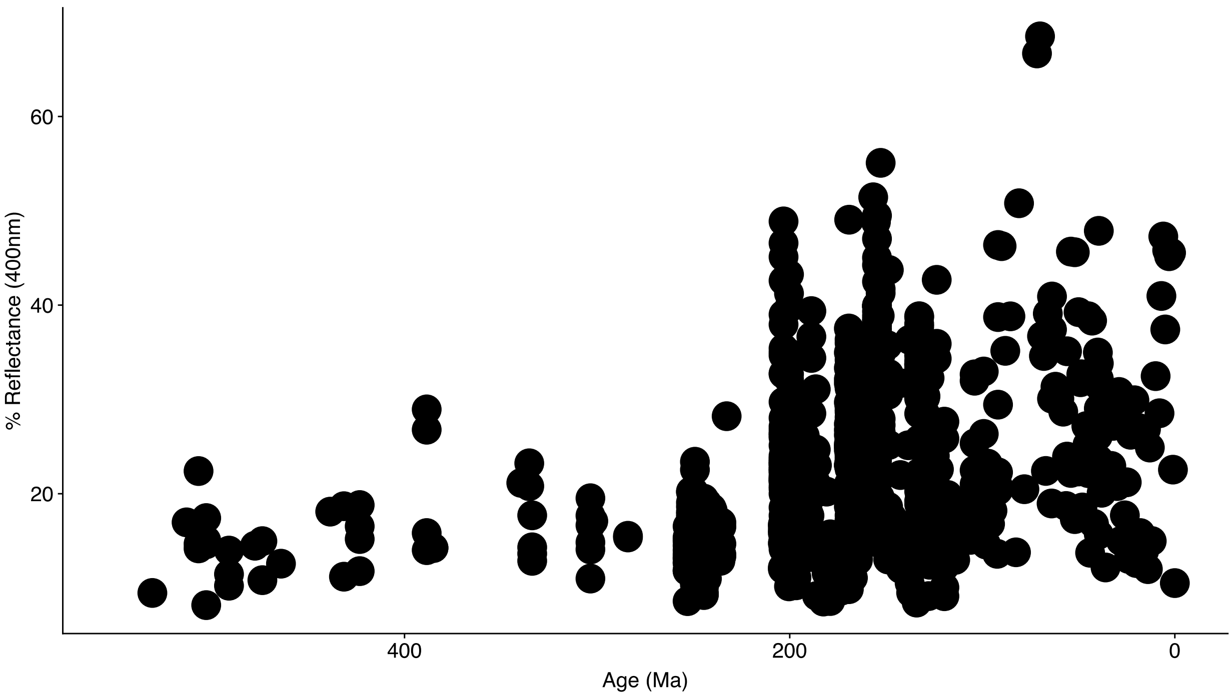


Figure 11 - Reflectance data at 400nm.

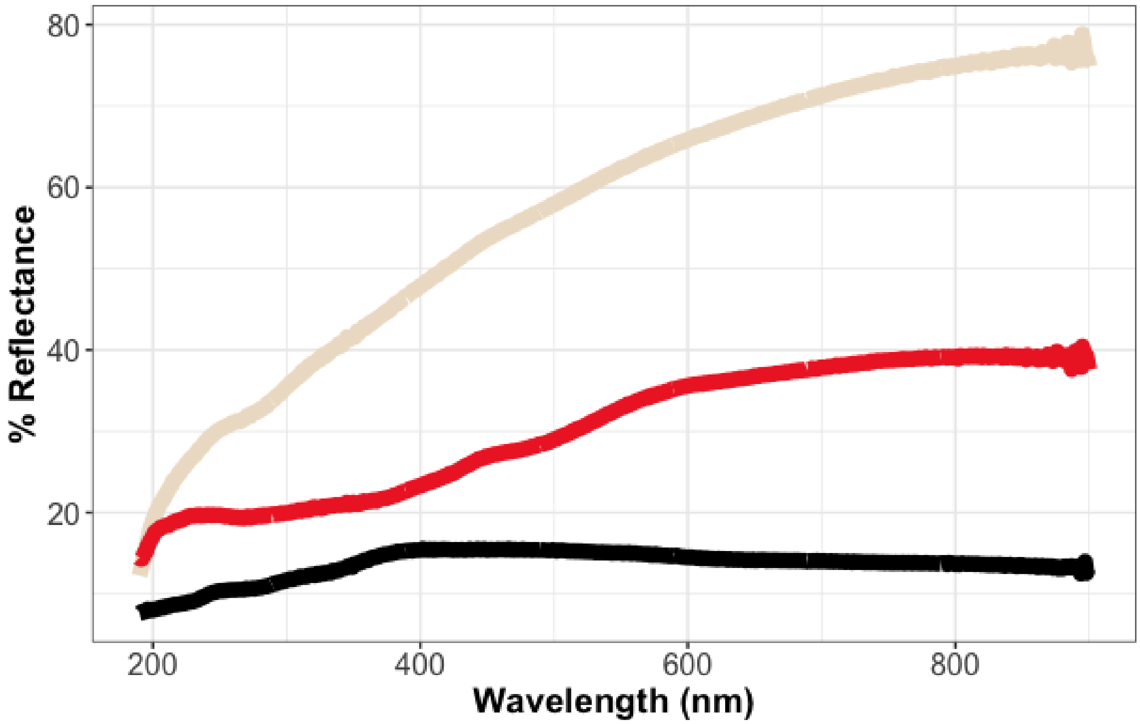


Figure 12 – Raw reflectance spectra for oxidized (top), grey (middle), and black (bottom) carbonate sediment samples.

APPENDIX B

SUPPLEMENTAL MATERIALS FOR CHAPTER 3

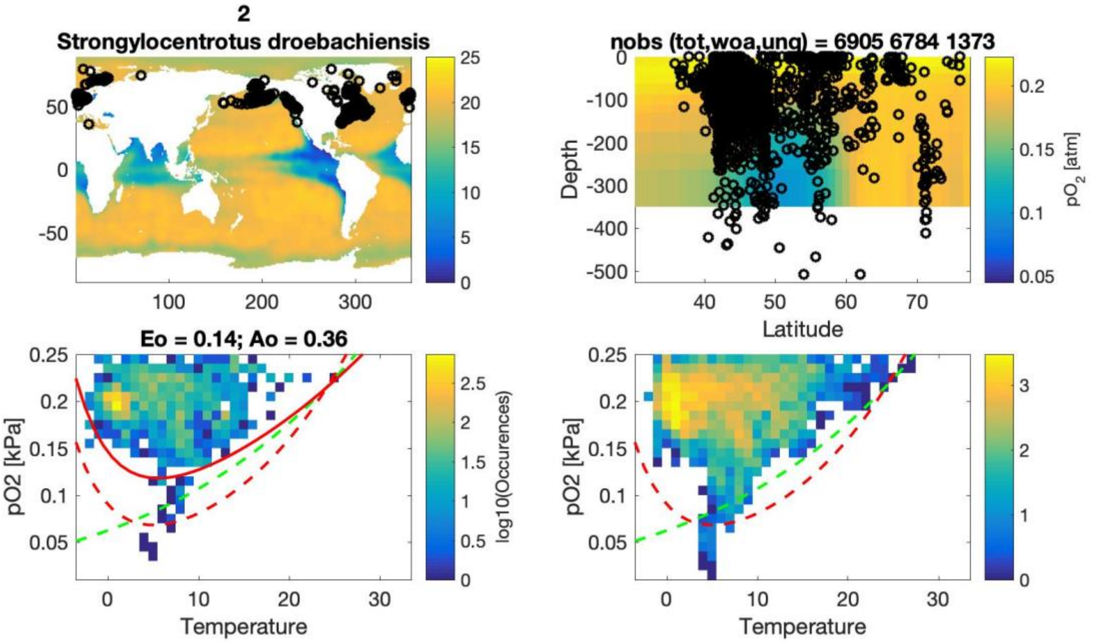
Table 1 – Initial distribution of metabolic data by taxonomy

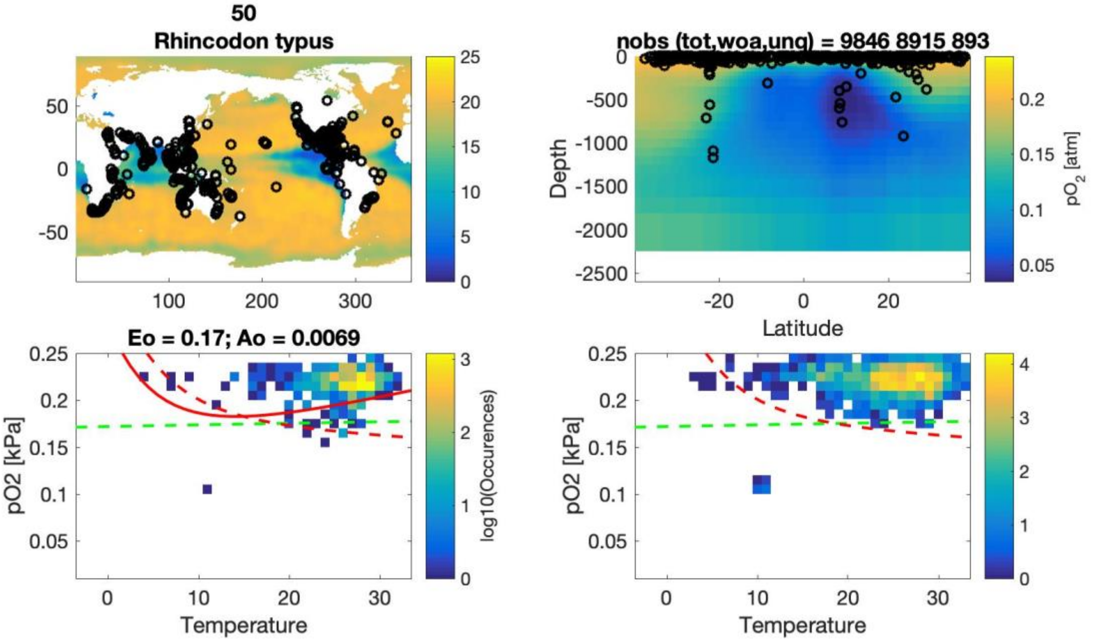
(Sub)-phylum	Ndata	Nspecies	Class	Ndata	Nspecies
Porifera	373	24	Hyalospongia	64	9
			Demospongiae	309	15
Cnidaria	1656	103	Hydrozoa	600	60
			Scyphozoa	867	26
			Anthozoa	189	17
Ctenophora	728	19	Ctenophora	728	19
Brachiopoda	558	28	Articulata	386	10
			Inarticulata	172	18
Plathelminthes	139	6	Turbellaria	139	6
Nemertea	145	4	Enopla	145	4
Rotifera	87	3	Rotifera	87	3
Nemata	608	62	Adenophorea	493	61
			Secernentea	115	1
Mollusca	6114	186	Aplacophora	3	1
			Polyplacophora	141	28
			Gastropoda	1716	39
			Bivalvia	3857	60
			Cephalopoda	397	58
Annelida	1141	60	Polychaeta	1124	56
			Pogonophora	17	4
Crustacea	8842	413	Branchiopoda	342	6
			Ostracoda	34	7
			Cirripedia	237	11
			Malacostraca	6661	255
			Copepoda	1587	134
Insecta	1096	13	Pterygota	1096	13
Chaetognatha	466	14	Chaetognatha	466	14
Echinodermata	3664	157	Asteroidea	1598	48
			Ophiuroidea	217	34
			Echinoidea	1343	31
			Holothuroidea	419	28
			Crinoidea	87	16
Tunicata	389	19	Ascidiacea	275	7
Thaliacea	90	11	Thaliacea	90	11

Vertebrata	1548	95	Chondricthys	169	13
			Actinopterygii	1212	51
			Sarcopterygii	130	26
			Myxini	37	5
Appendicularia	24	1	Appendicularia	24	1
Total	**27668**	**1218**			

APPENDIX C

SUPPLEMENTAL MATERIALS FOR CHAPTER 4





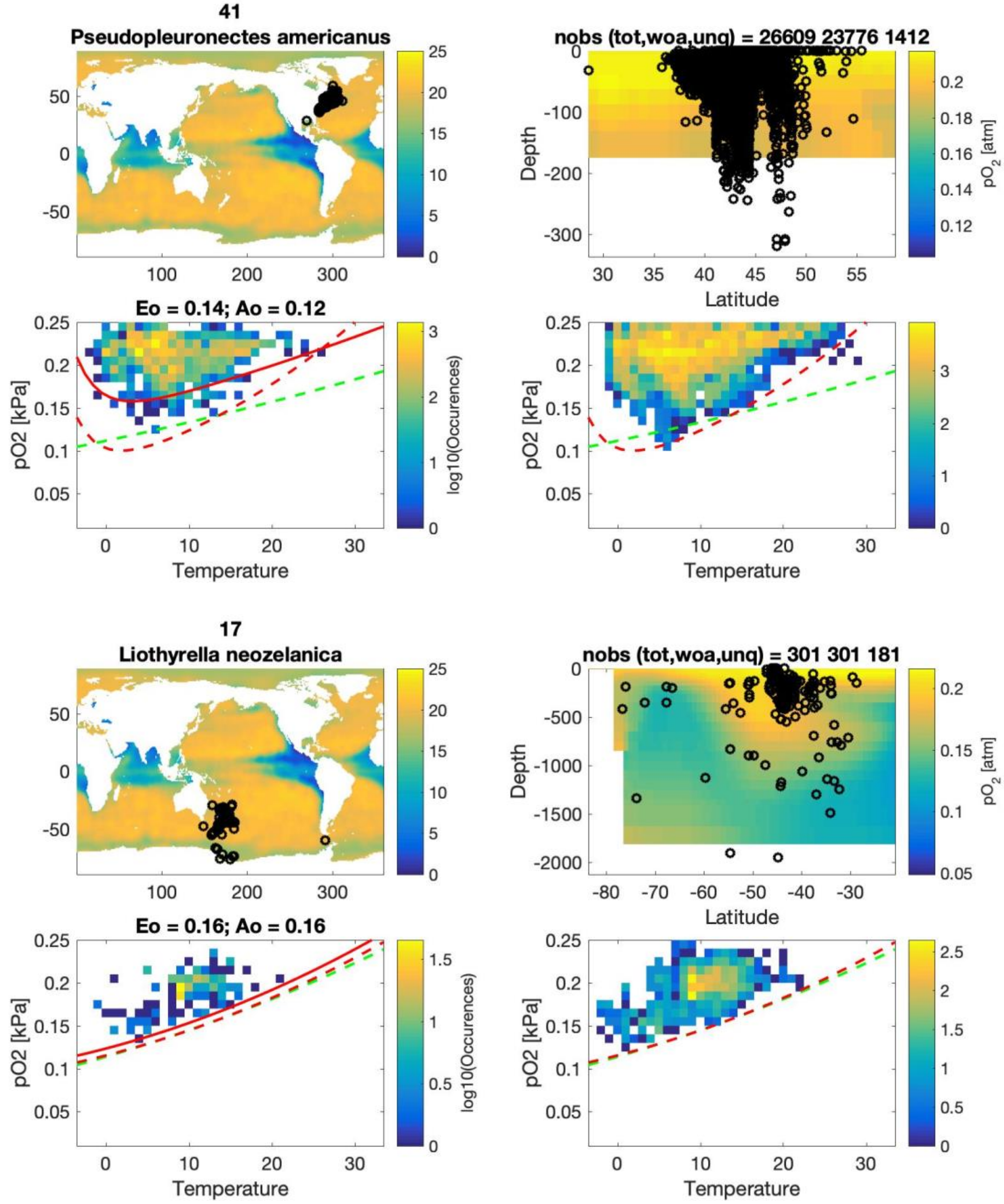


Figure 13 – Example of how distribution data is pulled from OBIS and utilized to construct metabolic index curves in four species. Species longitude and latitude (top left) and depth of occurrence (top right) is matched with climatological data. Data are plotted onto on temperature and oxygen state space. Green curves on bottom panels were used in this study and represent temperature vs pcrit curves inferred from species distribution data. Bottom left panel using climatological data only from the month of the year the species was reported. Bottom right panel uses temperature and pO_2 all months of the year from occurrence location.

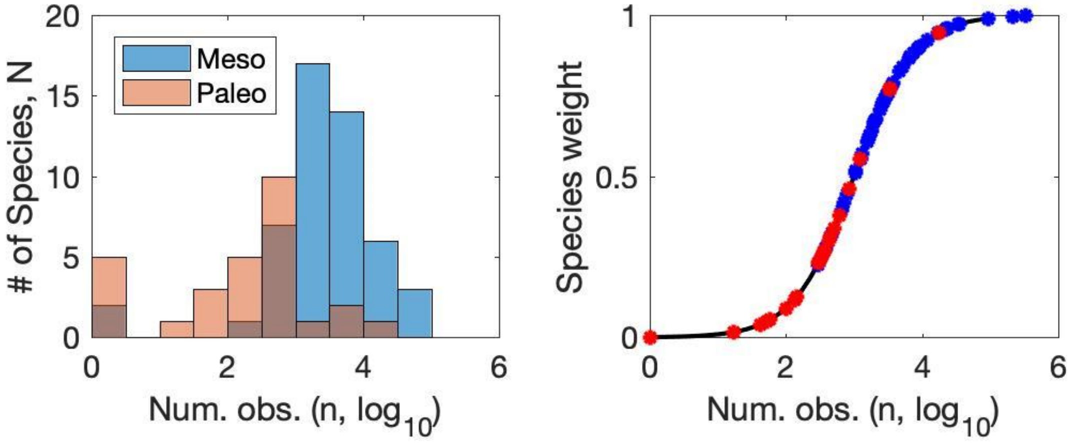


Figure 14 – Data used for weighting. Left panel shows number of data used to generate each plot. Right panel shows species weighting kernel.

Table 2 – Species used for Mesozoic and Cenozoic groupings.

Species Name	OBIS Species ID	Geologic Era
Glyptonotus antarcticus	174803	Paleozoic
Ophiacantha abnormis	244219	Paleozoic
Ophiacantha abyssicola	124973	Paleozoic
Ophiacantha aculetea	183310	Paleozoic
Monoplacophora Odhner	415	Paleozoic
Neopilina galatheae	343689	Paleozoic
Florometra Serratissima	714272	Paleozoic
Antedon bifida	124201	Paleozoic
Pleurotomariidae Swainson	196325	Paleozoic
Lepetelloidea dall	382160	Paleozoic
Pseudococculinidae Hickman	23106	Paleozoic
Solemya velum	156994	Paleozoic
Acharax johnsoni	293239	Paleozoic
Diplopteraster multipes	124128	Paleozoic
Hippasteria phrygiana	124043	Paleozoic
Lophaster fucifer	124156	Paleozoic
Liothyrella neozelanica	235459	Paleozoic
Liothyrella uva	231830	Paleozoic
Gryphus vitreus	104068	Paleozoic
Gyrothyris mawsoni	235675	Paleozoic
Microporina borealis	160496	Paleozoic
Dendrobeania murrayana	111174	Paleozoic
Schizoporella unicornis	111538	Paleozoic
Bathynomus giganteus	259252	Paleozoic
Bathynomus immanis	259253	Paleozoic
Lophelia pertusa	1245747	Paleozoic
Oculina varicosa	287102	Paleozoic
Latimeria chalumnae	217438	Paleozoic
Heliocidaris erythrogramma	513313	Mesozoic
Strongylocentrotus droebachiensis	124321	Mesozoic
Echinostrephus aciculatus	513245	Mesozoic
Dyspanopeus texanus	443955	Mesozoic
Dyspanopeus sayi	107412	Mesozoic
Persephona mediterranea	158443	Mesozoic
Jasus edwardsii	382879	Mesozoic
Jasus lalandii	246322	Mesozoic

Panulirus interruptus	382898	Mesozoic
Homarus americanus	156134	Mesozoic
Dipturus laevis	158548	Mesozoic
Rostroraja alba	105896	Mesozoic
Rajella fyllae	105894	Mesozoic
Pteroplatytrygon violacea	158540	Mesozoic
Torpedo marmorata	271684	Mesozoic
Trygonorrhina fasciata	283064	Mesozoic
Nucella lapillus	140403	Mesozoic
Reishia clavigera	397003	Mesozoic
Dicathais orbita	396664	Mesozoic
Euspira nitida	151894	Mesozoic
Mysia undata	140728	Mesozoic
Dosinia lupinus	141912	Mesozoic
Dosinia caerulea	507581	Mesozoic
Loligo reynaudii d'Orbigny	220316	Mesozoic
Doryteuthis (Amerigo) opalescens	410353	Mesozoic
Sepia officinalis	141444	Mesozoic
Sepia apama	342111	Mesozoic
Octopus vulgaris	140605	Mesozoic
Octopus joubini	341985	Mesozoic
Cirroteuthis muelleri	342212	Mesozoic
Magallana gigas	836033	Mesozoic
Crassostrea virginica	140657	Mesozoic
Ostrea edulis	140658	Mesozoic
Florometra serratissima	714272	Mesozoic
Comatula pectinata	246762	Mesozoic
Comactinia meridionalis	246741	Mesozoic
Cenolia trichoptera	246736	Mesozoic
Seriola lalandi	218436	Mesozoic
Kajikia audax	712907	Mesozoic
Oncorhynchus tshawytscha	158075	Mesozoic
Pseudopleuronectes americanus	158885	Mesozoic
Caranx melampygus	218419	Mesozoic
Holacanthus ciliaris	276012	Mesozoic
Sphyraena barracuda	345843	Mesozoic
Semicossyphus pulcher	282753	Mesozoic
Hypsypops rubicundus	281130	Mesozoic
Gadus chalcogrammus	300735	Mesozoic

Notorynchus cepedianus	217628	Mesozoic
Galeocerdo cuvier	105799	Mesozoic
Rhincodon typus	105847	Mesozoic
Callorhinchus callorynchus	278468	Mesozoic
Sphyrna lewini	105816	Mesozoic

REFERENCES

Ager, D. V. (1981). *The nature of the stratigraphical record*. Macmillan. https://books.google.com/books?id=9SwUAQAAIAAJ

Algeo, T. J., Luo, G. M., Song, H. Y., Lyons, T. W., & Canfield, D. E. (2015). Reconstruction of secular variation in seawater sulfate concentrations. *Biogeosciences*, *12*(7), 2131–2151. https://doi.org/10.5194/bg-12-2131-2015

Algeo, Thomas J., Heckel, P. H., Maynard, J. B., Blakey, R. C., & Rowe, H. (2008). Modern and ancient epeiric seas and the super-estuarine circulation model of marine anoxia. *Special Paper - Geological Association of Canada*, *48*, 7–38. https://www.academia.edu/9827968/Modern_and_ancient_epicratonic_seas_and_the_super estuarine_circulation_model_of_marine_anoxia_2008_Dynamics_of_Epeiric_Seas_

Aller, R. C. (1994). Bioturbation and remineralization of sedimentary organic matter: effects of redox oscillation. *Chemical Geology*, *114*(3–4), 331–345. https://doi.org/10.1016/0009-2541(94)90062-0

Allison, P. A., & Wells, M. R. (2006). Circulation in large ancient epicontinental seas: What was different and why? *Palaios*, *21*(6), 513–515. https://doi.org/10.2110/palo.2006.S06

Allmon, W. D., & Martin, R. E. (2014a). Seafood through time revisited: the Phanerozoic increase in marine trophic resources and its macroevolutionary consequences. *Paleobiology*, *40*(2), 256–287. https://doi.org/10.1666/13065

Allmon, W. D., & Martin, R. E. (2014b). Seafood through time revisited: the Phanerozoic increase in marine trophic resources and its macroevolutionary consequences. *Paleobiology*, *40*(02), 256–287. https://doi.org/10.1666/13065

Amemiya, C. T., Alfoldi, J., Lee, A. P., Fan, S., Philippe, H., MacCallum, I., Braasch, I., Manousaki, T., Schneider, I., Rohner, N., Organ, C., Chalopin, D., Smith, J. J., Robinson, M., Dorrington, R. A., Gerdol, M., Aken, B., Biscotti, M. A., Barucca, M., … Lindblad-Toh, K. (2013). The African coelacanth genome provides insights into tetrapod evolution. *Nature*, *496*(7445), 311–316. https://doi.org/10.1038/nature12027

Ameziane, N., & Roux, M. (1997). Biodiversity and historical biogeography of stalked crinoids (Echinodermata) in the deep sea. *Biodiversity and Conservation*, *6*(11), 1557–1570. https://doi.org/10.1023/A:1018370620870

Anbar, A. D., Duan, Y., Lyons, T. W., Arnold, G. L., Kendall, B., Creaser, R. a, Kaufman, A. J., Gordon, G. W., Scott, C., Garvin, J., & Buick, R. (2007). A whiff of oxygen before the great oxidation event? *Science (New York, N.Y.)*, *317*(5846), 1903–1906. https://doi.org/10.1126/science.1140325

Arvidson, R. S. (2006). MAGic: A Phanerozoic Model for the Geochemical Cycling of Major

Rock-Forming Components. *American Journal of Science*, *306*(3), 135–190. https://doi.org/10.2475/ajs.306.3.135

Ausich, W. I., & Bottjer, D. J. (1982). Tiering in suspension-feeding communities on soft substrata throughout the Phanerozoic. *Science*, *216*(4542), 173–174. https://doi.org/10.1126/science.216.4542.173

BA Seibel, J. D. (2007). The rate of metabolism in marine animals: environmental constraints, ecological demands and energetic opportunities. *Phil. Trans. R. Soc. Lond. B*, *362*, 2061–2078.

Bambach, R. K. (1993). Seafood through time: Changes in biomass, energetics, and productivity in the marine ecosystem. *Paleobiology*, *3*(N/A), 372–397. https://doi.org/10.1017/S0094837300000336

Belcher, C. M., & McElwain, J. C. (2008). Limits for Combustion in Low O2 Redefine Paleoatmospheric Predictions for the Mesozoic. *Science*, *321*(5893), 1197–1200. https://doi.org/10.1126/science.1160978

Belcher, Claire M, Yearsley, J. M., Hadden, R. M., McElwain, J. C., & Rein, G. (2010). Baseline intrinsic flammability of Earth's ecosystems estimated from paleoatmospheric oxygen over the past 350 million years. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(52), 22448–22453. https://doi.org/10.1073/pnas.1011974107

Berner, R. A. (2009). Phanerozoic atmospheric oxygen: New results using the GEOCARBSULF model. *American Journal of Science*, *309*(7), 603–606. https://doi.org/10.2475/07.2009.03

Berner, R. a., Berner, R. a., VandenBrooks, J. M., VandenBrooks, J. M., Ward, P. D., & Ward, P. D. (2005). Oxygen and evolution. *Science*, *316*(April), 557–558. http://scholar.google.com/scholar?hl=en&btnG=Search&q=intitle:Oxygen+and+Evolution#0

Berner, R. A., & Westrich, J. T. (1985). Bioturbation and the early diagenesis of carbon and sulfur. *American Journal of Science*, *285*(3), 193–206. https://doi.org/10.2475/ajs.285.3.193

Berner, Robert A. (2006). GEOCARBSULF: A combined model for Phanerozoic atmospheric O2 and CO2. *Geochimica et Cosmochimica Acta*, *70*(23), 5653–5664. https://doi.org/10.1016/j.gca.2005.11.032

Berner, Robert A. (1984). Sedimentary pyrite formation: An update. *Geochimica et Cosmochimica Acta*, *48*(4), 605–615. https://doi.org/10.1016/0016-7037(84)90089-9

Bertrand, P., & Lallier-Vergès, E. (1993). Past sedimentary organic matter accumulation and degradation controlled by productivity. *Nature*, *364*(6440), 786–788. https://doi.org/10.1038/364786a0

Bottjer, D. J., & Ausich, W. I. (1986). Phanerozoic development of tiering in soft substrata suspension-feeding communities. *Paleobiology*, *4*(4), 400–420. https://doi.org/10.1017/S0094837300003134

Bowles, M. W., Mogollon, J. M., Kasten, S., Zabel, M., & Hinrichs, K.-U. (2014). Global rates of marine sulfate reduction and implications for sub-sea-floor metabolic activities. *Science*, *344*(6186), 889–891. https://doi.org/10.1126/science.1249213

Boynton, W., & Kemp, W. (1985). Nutrient regeneration and oxygen consumption by sediments along an estuarine salinity gradient. *Marine Ecology Progress Series*, *23*, 45–55. https://doi.org/10.3354/meps023045

Bretsky, P. W. (1969). Evolution of Paleozoic benthic marine invertebrate communities. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *6*(C), 45–59. https://doi.org/10.1016/0031-0182(69)90003-0

Brett, C. E. (1984). The mid-Paleozoic precursor to the Mesozoic marine revolution. *Paleobiology*, *10*(2), 229–245. https://doi.org/10.1017/S0094837300008174

Brey, T. (2001). Population dynamics in benthic invertebrates. A virtual handbook. *EPIC3http://Www.Awi-Bremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/Main.Html. Alfred Wegener Institute for Polar and Marine Research, Germany*.

Brey, T. (2010). An empirical model for estimating aquatic invertebrate respiration. *Methods in Ecology and Evolution*, *1*(1), 92–101. https://doi.org/10.1111/j.2041-210x.2009.00008.x

Brown, A., Hauton, C., Stratmann, T., Sweetman, A., van Oevelen, D., & Jones, D. O. B. (2018a). Metabolic rates are significantly lower in abyssal Holothuroidea than in shallow-water Holothuroidea. *Royal Society Open Science*, *5*(5). https://doi.org/10.1098/rsos.172162

Brown, A., Hauton, C., Stratmann, T., Sweetman, A., van Oevelen, D., & Jones, D. O. B. (2018b). Metabolic rates are significantly lower in abyssal Holothuroidea than in shallow-water Holothuroidea. *Royal Society Open Science*, *5*(5). https://doi.org/10.1098/rsos.172162

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004a). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004b). Toward a metabolic theory of ecology. *Ecology*, *85*(7), 1771–1789. https://doi.org/10.1890/03-9000

Brumsack, H.-J. (2006). The trace metal content of recent organic carbon-rich sediments: Implications for Cretaceous black shale formation. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *232*(2–4), 344–361. https://doi.org/10.1016/j.palaeo.2005.05.011

Brunton, F. R., & Dixon, O. A. (1994). Siliceous sponge-microbe biotic associations and their recurrence through the Phanerozoic as reef mound constructors. *Palaios*, *9*(4), 370–387. https://doi.org/10.2307/3515056

The Mesozoic Marine Revolution, Topics in Geobiology 19 (2016). https://doi.org/10.1007/978-94-017-9597-5_2

Buatois, L. A., Carmona, N. B., Curran, H. A., Netto, R. G., Mángano, M. G., & Wetzel, A. (2016a). The Mesozoic Marine Revolution. In *Topics in Geobiology* (Vol. 40, pp. 19–134). Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9597-5_2

Buatois, L. A., Carmona, N. B., Curran, H. A., Netto, R. G., Mángano, M. G., & Wetzel, A. (2016b). The Mesozoic Marine Revolution. In *Topics in Geobiology* (Vol. 40, pp. 19–134). Springer, Dordrecht. https://doi.org/10.1007/978-94-017-9597-5_2

Buick, R. (2008). When did oxygenic photosynthesis evolve? *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1504), 2731–2743. https://doi.org/10.1098/rstb.2008.0041

Bush, A. M., & Bambach, R. K. (2011a). Paleoecologic megatrends in marine metazoa. *Annual Review of Earth and Planetary Sciences*, *39*, 241–269. https://doi.org/10.1146/annurev-earth-040809-152556

Bush, A. M., & Bambach, R. K. (2011b). Paleoecologic Megatrends in Marine Metazoa. *Annual Review of Earth and Planetary Sciences*, *39*(1), 241–269. https://doi.org/10.1146/annurev-earth-040809-152556

C Deutsch, A. F. B. S. H.-O. P. R. H. (2015). Ecophysiology. Climate change tightens a metabolic constraint on marine habitats. *Science*, *348*, 1132–1135.

Cai, W.-J., & Sayles, F. L. (1996). Oxygen penetration depths and fluxes in marine sediments. *Marine Chemistry*, *52*(2), 123–131. https://doi.org/10.1016/0304-4203(95)00081-X

Calvert, S. E. (1987). Oceanographic controls on the accumulation of organic matter in marine sediments. *Geological Society, London, Special Publications*, *26*(1), 137–151. https://doi.org/10.1144/GSL.SP.1987.026.01.08

Canfield, D. E., & Farquhar, J. (2009). Animal evolution, bioturbation, and the sulfate concentration of the oceans. *Proceedings of the National Academy of Sciences*, *106*(20), 8123–8127. https://doi.org/10.1073/pnas.0902037106

Canfield, Donald E. (1989). Reactive iron in marine sediments. *Geochimica et Cosmochimica Acta*, *53*(3), 619–632. https://doi.org/10.1016/0016-7037(89)90005-7

Canfield, Donald E. (1993). Organic Matter Oxidation in Marine Sediments. In *Interactions of C, N, P and S Biogeochemical Cycles and Global Change* (pp. 333–363). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-76064-8_14'

Canfield, Donald E. (1994). Factors influencing organic carbon preservation in marine sediments. *Chemical Geology*, *114*(3–4), 315–329. https://doi.org/10.1016/0009-2541(94)90061-2

Canfield, Donald E. (1998). A new model for Proterozoic ocean chemistry. *Nature*, *396*(December), 450–453. https://doi.org/10.1038/24839

Canfield, Donald E, Ngombi-Pemba, L., Hammarlund, E. U., Bengtson, S., Chaussidon, M., Gauthier-Lafaye, F., Meunier, A., Riboulleau, A., Rollion-Bard, C., Rouxel, O., Asael, D., Pierson-Wickmann, A.-C., & El Albani, A. (2013). Oxygen dynamics in the aftermath of the Great Oxidation of Earth's atmosphere. *Proceedings of the National Academy of Sciences of the United States of America*, *110*(42), 16736–16741. https://doi.org/10.1073/pnas.1315570110

Chamberlain, S. C., Meyer-Rochow, V. B., & Dossert, W. P. (1986). Morphology of the compound eye of the giant deep-sea isopodBathynomus giganteus. *Journal of Morphology*, *189*(2), 145–156. https://doi.org/10.1002/jmor.1051890205

Clement, A. M., & Long, J. A. (2010). Air-breathing adaptation in a marine Devonian lungfish. *Biology Letters*, *6*(4), 509–512. https://doi.org/10.1098/rsbl.2009.1033

Dahl, T. W., Boyle, R. a., Canfield, D. E., Connelly, J. N., Gill, B. C., Lenton, T. M., & Bizzarro, M. (2014). Uranium isotopes distinguish two geochemically distinct stages during the later Cambrian SPICE event. *Earth and Planetary Science Letters*, *401*, 313–326. https://doi.org/10.1016/j.epsl.2014.05.043

Dahl, T. W., Hammarlund, E. U., Anbar, A. D., Bond, D. P. G., Gill, B. C., Gordon, G. W., Knoll, A. H., Nielsen, A. T., Schovsbo, N. H., & Canfield, D. E. (2010a). Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(42), 17911–17915. https://doi.org/10.1073/pnas.1011287107

Dahl, T. W., Hammarlund, E. U., Anbar, A. D., Bond, D. P. G., Gill, B. C., Gordon, G. W., Knoll, A. H., Nielsen, A. T., Schovsbo, N. H., & Canfield, D. E. (2010b). Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(42), 17911–17915. https://doi.org/10.1073/pnas.1011287107

de Boyer Montégut, C. (2004). Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. *Journal of Geophysical Research*, *109*(C12), C12003. https://doi.org/10.1029/2004JC002378

Deutsch, C., Penn, J. L., & Seibel, B. (2020). Metabolic trait diversity shapes marine biogeography. *Nature*, *585*, 1–6. https://doi.org/10.1038/s41586-020-2721-y

Diaz, R. J., & Rosenberg, R. (2008). Spreading Dead Zones and Consequences for Marine Ecosystems. *Science*, *321*(5891), 926–929. https://doi.org/10.1126/science.1156401

Diaz, Robert J, & Rosenberg, R. (1995). Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology. An Annual Review*, *33*, 203–245.

Diester-Haass, L., Meyers, P. A., & Bickert, T. (2004). Carbonate crash and biogenic bloom in the late Miocene: Evidence from ODP Sites 1085, 1086, and 1087 in the Cape Basin, southeast Atlantic Ocean. *Paleoceanography*, *19*(1), n/a-n/a. https://doi.org/10.1029/2003PA000933

Drazen, J. C., & Seibel, B. A. (2007). Depth-related trends in metabolism of benthic and benthopelagic deep-sea fishes. *Limnology and Oceanography*, *52*(5), 2306–2316. https://doi.org/10.4319/lo.2007.52.5.2306

Droser, M. L., & Bottjer, D. J. (1989). Ordovician increase in extent and depth of bioturbation: Implications for understanding early Paleozoic ecospace utilization. *Geology*, *17*(9), 850. https://doi.org/10.1130/0091-7613(1989)017<0850:OIIEAD>2.3.CO;2

Droser, M. L., & Finnegan, S. (2003). The Ordovician radiation: A follow-up to the Cambrian explosion? *Integrative and Comparative Biology*, *43*(1), 178–184. https://doi.org/10.1093/icb/43.1.178

Dunne, J. A., Williams, R. J., Martinez, N. D., Wood, R. A., & Erwin, D. H. (2008). Compilation and Network Analyses of Cambrian Food Webs. *PLoS Biology*, *6*(4), e102. https://doi.org/10.1371/journal.pbio.0060102

Eléaume, M., Bohn, J. M., Roux, M., & Améziane, N. (2012). Stalked crinoids (Echinodermata) collected by the R/V Polarstern and Meteor in the south Atlantic and in Antarctica. *Zootaxa*, *3425*(3425), 1–22. https://doi.org/10.11646/zootaxa.3425.1.1

Falkowski, P. G. (2005). The Rise of Oxygen over the Past 205 Million Years and the Evolution of Large Placental Mammals. *Science*, *309*(5744), 2202–2204. https://doi.org/10.1126/science.1116047

Falkowski, P., & Knoll, A. H. (2007). Evolution of primary producers in the sea. In *Evolution of Primary Producers in the Sea*. Elsevier Inc. https://doi.org/10.1016/B978-0-12-370518-1.X5000-0

Falkowski, Paul G., Schofield, O., Katz, M. E., Van de Schootbrugge, B., & Knoll, A. H. (2004). Why is the Land Green and the Ocean Red? In *Coccolithophores* (pp. 429–453). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-662-06278-4_16

Farquhar, J. (2000). Atmospheric Influence of Earth's Earliest Sulfur Cycle. *Science*, *289*(5480), 756–758. https://doi.org/10.1126/science.289.5480.756

Fennel, K., Follows, M., & Falkowski, P. G. (2005). The co-evolution of the nitrogen, carbon and oxygen cycles in the proterozoic ocean. *American Journal of Science*, *305*(6-8 SPEC. ISS.), 526–545. https://doi.org/10.2475/ajs.305.6-8.526

Filippelli, G. M., Sierro, F. J., Flores, J. A., Vázquez, A., Utrilla, R., Pérez-Folgado, M., & Latimer, J. C. (2003). A sediment–nutrient–oxygen feedback responsible for productivity variations in Late Miocene sapropel sequences of the western Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *190*, 335–348. https://doi.org/10.1016/S0031-0182(02)00613-2

Finnegan, S. (2013). Quantifying Seafood Through Time: Counting Calories in the Fossil Record. *The Paleontological Society Papers*, *19*, 21–50. https://doi.org/10.1017/s1089332600002679

Finnegan, S., McClain, C. M., Kosnik, M. a, & Payne, J. L. (2011). Escargots through time: an energetic comparison of marine gastropod assemblages before and after the Mesozoic Marine Revolution. *Paleobiology*, *37*(2), 252–269. https://doi.org/10.1666/09066.1

Franks, P. J. S. (2015). Has Sverdrup's critical depth hypothesis been tested? Mixed layers vs. turbulent layers. *ICES Journal of Marine Science*, *72*(6), 1897–1907. https://doi.org/10.1093/icesjms/fsu175

Froese, R. and Pauly, D. (2020) Fish Base. World Wide Web Electronic Publication. www.fishbase.org - References - Scientific Research Publishing. (n.d.). Retrieved December 18, 2020, from https://www.scirp.org/(S(oyulxb452alnt1aej1nfow45))/reference/ReferencesPapers.aspx?ReferenceID=2092723

Gallo, N., Beckwith, M., Wei, C., Levin, L., Kuhnz, L., & Barry, J. (2020). Dissolved oxygen and temperature best predict deep-sea fish community structure in the Gulf of California with climate change implications. *Marine Ecology Progress Series*, *637*, 159–180. https://doi.org/10.3354/meps13240

Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M., & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, *293*(5538), 2248–2251. https://doi.org/10.1126/science.1061967

Gillooly, James F., Gomez, J. P., Mavrodiev, E. V., Rong, Y., & McLamore, E. S. (2016). Body mass scaling of passive oxygen diffusion in endotherms and ectotherms. *Proceedings of the National Academy of Sciences*, *113*(19), 5340–5345. https://doi.org/10.1073/pnas.1519617113

Giosan, L., Flood, R. D., Grützner, J., & Mudie, P. (2002). Paleoceanographic significance of sediment color on western North Atlantic Drifts: II. Late Pliocene-Pleistocene sedimentation. *Marine Geology*, *189*(1–2), 43–61. https://doi.org/10.1016/S0025-3227(02)00322-5

Glasspool, I. J., & Scott, A. C. (2010). Phanerozoic concentrations of atmospheric oxygen reconstructed from sedimentary charcoal. *Nature Geoscience*, *3*(9), 627–630. https://doi.org/10.1038/ngeo923

Glover, A. G., & Smith, C. R. (2003). The deep-sea floor ecosystem: Current status and prospects of anthropogenic change by the year 2025. In *Environmental Conservation* (Vol. 30, Issue 3, pp. 219–241). Cambridge University Press. https://doi.org/10.1017/S0376892903000225

Goldberg, S. L., Present, T. M., Finnegan, S., & Bergmann, K. D. (2021). A high-resolution record of early Paleozoic climate. *Proceedings of the National Academy of Sciences*, *118*(6), e2013083118. https://doi.org/10.1073/pnas.2013083118

Goldblatt, C., Lenton, T. M., & Watson, A. J. (2006). Bistability of atmospheric oxygen and the Great Oxidation. *Nature*, *443*(7112), 683–686. https://doi.org/10.1038/nature05169

Harper, E. M. (2003). The Mesozoic Marine Revolution. In *Predator—Prey Interactions in the Fossil Record* (pp. 433–455). Springer US. https://doi.org/10.1007/978-1-4615-0161-9_19

Harris, P. T. (2014). Shelf and deep-sea sedimentary environments and physical benthic disturbance regimes: A review and synthesis. In *Marine Geology* (Vol. 353, pp. 169–184). Elsevier. https://doi.org/10.1016/j.margeo.2014.03.023

Harrison, J. F., Kaiser, A., & VandenBrooks, J. M. (2010). Atmospheric oxygen level and the evolution of insect body size. *Proceedings. Biological Sciences / The Royal Society*, *277*(1690), 1937–1946. https://doi.org/10.1098/rspb.2010.0001

Hartnett, H. E., Keil, R. G., Hedges, J. I., & Devol, A. H. (1998). Influence of oxygen exposure time on organic carbon preservation in continental margin sediments. *Nature*, *391*(6667), 572–575. https://doi.org/10.1038/35351

Hatton, I. A., Dobson, A. P., Storch, D., Galbraith, E. D., & Loreau, M. (2019). Linking scaling laws across eukaryotes. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(43), 21616–21622. https://doi.org/10.1073/pnas.1900492116

Hearing, T. W., Harvey, T. H. P., Williams, M., Leng, M. J., Lamb, A. L., Wilby, P. R., Gabbott, S. E., Pohl, A., & Donnadieu, Y. (2018). An early Cambrian greenhouse climate. *Science Advances*, *4*(5), 5690. https://doi.org/10.1126/sciadv.aar5690

Heim, N. A., Knope, M. L., Schaal, E. K., Wang, S. C., & Payne, J. L. (2015). Cope's rule in the evolution of marine animals. *Science*, *347*(6224), 867–870. https://doi.org/10.1126/science.1260065

Heim, Noel A., Bakshi, S. H., Buu, L., Chen, S., Heh, S., Jain, A., Noll, C., Patkar, A., Rizk, N., Sundararajan, S., Villante, I., Knope, M. L., & Payne, J. L. (2020). Respiratory medium and circulatory anatomy constrain size evolution in marine macrofauna. *Paleobiology*, *46*(3), 288–303. https://doi.org/10.1017/pab.2020.16

Heim, Noel A., & Knope, M. (2015). Cope's rule in the evolution of marine animals. *Science*, *347*(6224), 867–870. https://doi.org/10.1126/science.1260065

Henrichs, S. M. (1992). Early diagenesis of organic matter in marine sediments: progress and perplexity. *Marine Chemistry*, *39*(1–3), 119–149. https://doi.org/10.1016/0304-4203(92)90098-U

Holland, H. D. (2006). The Oxygenation of the aAtmosphere and Oceans. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *361*(1470), 903–915. https://doi.org/10.1098/rstb.2006.1838

Huntley, J. W., & Kowalewski, M. (2007). Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(38), 15006–15010. https://doi.org/10.1073/pnas.0704960104

Ingall, E., & Jahnke, R. (1994). Evidence for enhanced phosphorus regeneration from marine sediments overlain by oxygen depleted waters. In *Geochimica et Cosmochimica Acta* (Vol. 58, Issue 11, pp. 2571–2575). Pergamon. https://doi.org/10.1016/0016-7037(94)90033-7

Jenkyns, H. C. (1980). Cretaceous anoxic events: from continents to oceans. *Journal of the Geological Society*, *137*(2), 171–188. https://doi.org/10.1144/gsjgs.137.2.0171

Jenkyns, Hugh C. (2010a). Geochemistry of oceanic anoxic events. *Geochemistry, Geophysics, Geosystems*, *11*(3), n/a-n/a. https://doi.org/10.1029/2009GC002788

Jenkyns, Hugh C. (2010b). Geochemistry of oceanic anoxic events. *Geochemistry, Geophysics, Geosystems*, *11*(3). https://doi.org/10.1029/2009GC002788

Jørgensen, B. B. (1982). Mineralization of organic matter in the sea bed—the role of sulphate reduction. *Nature*, *296*(5858), 643–645. https://doi.org/10.1038/296643a0

Judd, E. J., Bhattacharya, T., & Ivany, L. C. (2020). A Dynamical Framework for Interpreting Ancient Sea Surface Temperatures. *Geophysical Research Letters*, *47*(15). https://doi.org/10.1029/2020GL089044

Keeling, R. E., Körtzinger, A., & Gruber, N. (2010). Ocean deoxygenation in a warming world. *Annual Review of Marine Science*, *2*, 199–229. https://doi.org/10.1146/annurev.marine.010908.163855

Knoll, A. H., & Follows, M. J. (2016a). A bottom-up perspective on ecosystem change in Mesozoic oceans. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1841). https://doi.org/10.1098/rspb.2016.1755

Knoll, A. H., & Follows, M. J. (2016b). A bottom-up perspective on ecosystem change in Mesozoic oceans. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1841), 20161755. https://doi.org/10.1098/rspb.2016.1755

Kocsis, Á. T., Reddin, C. J., Alroy, J., & Kiessling, W. (2019). The r package divDyn for quantifying diversity dynamics using fossil sampling data. *Methods in Ecology and Evolution*, *10*(5), 735–743. https://doi.org/10.1111/2041-210X.13161

Kocsis, A. T., Reddin, C. J., & Kiessling, W. (n.d.). *Handout to the R package divDyn v0.8.0 for diversity dynamics using fossil sampling data*. Retrieved December 11, 2020, from http://fossilworks.org

Korte, C., Hesselbo, S. P., Ullmann, C. V., Dietl, G., Ruhl, M., Schweigert, G., & Thibault, N. (2015). Jurassic climate mode governed by ocean gateway. *Nature Communications*, *6*(1), 1–7. https://doi.org/10.1038/ncomms10015

Krause, A. J., Mills, B. J. W., Zhang, S., Planavsky, N. J., Lenton, T. M., & Poulton, S. W. (2018). Stepwise oxygenation of the Paleozoic atmosphere. *Nature Communications*, *9*(1), 1–10. https://doi.org/10.1038/s41467-018-06383-y

Kristensen, E. (2000). Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. In *Life at Interfaces and Under Extreme Conditions* (pp. 1–24). Springer Netherlands. https://doi.org/10.1007/978-94-011-4148-2_1

Lalonde, K., Mucci, A., Ouellet, A., & Gélinas, Y. (2012). Preservation of organic matter in sediments promoted by iron. *Nature, 483*(7388), 198–200. https://doi.org/10.1038/nature10855

Lampitt, R. S., & Antia, A. N. (1997). Particle flux in deep seas: Regional characteristics and temporal variability. *Deep-Sea Research Part I: Oceanographic Research Papers*, *44*(8), 1377–1403. https://doi.org/10.1016/S0967-0637(97)00020-4

Leavitt, W. D., Halevy, I., Bradley, A. S., & Johnston, D. T. (2013). Influence of sulfate reduction rates on the Phanerozoic sulfur isotope record. *Proceedings of the National Academy of Sciences*, *110*(28), 11244–11249. https://doi.org/10.1073/pnas.1218874110

Lenton, T. M. (2001). The role of land plants, phosphorus weathering and fire in the rise and regulation of atmospheric oxygen. *Global Change Biology*, *7*(6), 613–629.

Lenton, T. M., Boyle, R. A., Poulton, S. W., Shields-Zhou, G. A., & Butterfield, N. J. (2014). Co-evolution of eukaryotes and ocean oxygenation in the Neoproterozoic era. In *Nature Geoscience* (Vol. 7, Issue 4, pp. 257–265). Nature Publishing Group. https://doi.org/10.1038/ngeo2108

Levin, L. A., & Gage, J. D. (1998). Relationships between oxygen, organic matter and the diversity of bathyal macrofauna. *Deep-Sea Research Part II: Topical Studies in Oceanography*, *45*(1–3), 129–163. https://doi.org/10.1016/S0967-0645(97)00085-4

Leys, S., Wilson, K., Holeton, C., Reiswig, H., Austin, W., & Tunnicliffe, V. (2004). Patterns of glass sponge (Porifera, Hexactinellida) distribution in coastal waters of British Columbia, Canada. *Marine Ecology Progress Series*, *283*, 133–149. https://doi.org/10.3354/meps283133

Lind, E. M., Vincent, J. B., Weiblen, G. D., Cavender-Bares, J., & Borer, E. T. (2015). Trophic phylogenetics: evolutionary influences on body size, feeding, and species associations in grassland arthropods. *Ecology*, *96*(4), 998–1009. https://doi.org/10.1890/14-0784.1

Lu, W., Ridgwell, A., Thomas, E., Hardisty, D. S., Luo, G., Algeo, T. J., Saltzman, M. R., Gill, B. C., Shen, Y., Ling, H. F., Edwards, C. T., Whalen, M. T., Zhou, X., Gutchess, K. M., Jin, L., Rickaby, R. E. M., Jenkyns, H. C., Lyons, T. W., Lenton, T. M., … Lu, Z. (2018). Late inception of a resiliently oxygenated upper ocean. *Science*, *361*(6398), 174–177. https://doi.org/10.1126/science.aar5372

Lu, Z., Hoogakker, B. A. A., Hillenbrand, C.-D., Zhou, X., Thomas, E., Gutchess, K. M., Lu, W., Jones, L., & Rickaby, R. E. M. (2016). Oxygen depletion recorded in upper waters of the glacial Southern Ocean. *Nature Communications*, *7*, 11146. https://doi.org/10.1038/ncomms11146

Lu, Z., Jenkyns, H. C., & Rickaby, R. E. M. (2010). Iodine to calcium ratios in marine carbonate as a paleo-redox proxy during oceanic anoxic events. *Geology*, *38*(12), 1107–1110. https://doi.org/10.1130/G31145.1

Lyle, M. (1983). The brown-green color transition in marine sediments: A marker of the Fe(III)-Fe(II) redox boundary1. *Limnology and Oceanography*, *28*(5), 1026–1033. https://doi.org/10.4319/lo.1983.28.5.1026

Lyons, T. W., Reinhard, C. T., & Planavsky, N. J. (2014). The rise of oxygen in Earth’s early ocean and atmosphere. *Nature*, *506*(7488), 307–315. https://doi.org/10.1038/nature13068

Makarieva, A. M., Gorshkov, V. G., Li, B.-L., Chown, S. L., Reich, P. B., & Gavrilov, V. M. (2008). Mean mass-specific metabolic rates are strikingly similar across life’s major domains: Evidence for life’s metabolic optimum. *Proceedings of the National Academy of Sciences*, *105*(44), 16994–16999. https://doi.org/10.1073/pnas.0802148105

Martin, R. E., & Servais, T. (2020). Did the evolution of the phytoplankton fuel the diversification of the marine biosphere? *Lethaia*, *53*(1), 5–31. https://doi.org/10.1111/let.12343

McClain, C. R., Allen, A. P., Tittensor, D. P., & Rex, M. A. (2012). Energetics of life on the deep seafloor. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(38), 15366–15371. https://doi.org/10.1073/pnas.1208976109

Meyer, K. M., Ridgwell, A., & Payne, J. L. (2016). The influence of the biological pump on ocean chemistry: Implications for long-term trends in marine redox chemistry, the global carbon cycle, and marine animal ecosystems. *Geobiology*, *14*(3), 207–219. https://doi.org/10.1111/gbi.12176

Meyers, S. R. (2007). Production and preservation of organic matter: The significance of iron. *Paleoceanography*, *22*(4), n/a-n/a. https://doi.org/10.1029/2006PA001332

Mills, B. J. W., Belcher, C. M., Lenton, T. M., & Newton, R. J. (2016). A modeling case for high atmospheric oxygen concentrations during the Mesozoic and Cenozoic. *Geology*, *44*(12), 1023–1026. https://doi.org/10.1130/G38231.1

Mills, B., Lenton, T. M., & Watson, A. J. (2014). Proterozoic oxygen rise linked to shifting balance between seafloor and terrestrial weathering. *Proceedings of the National Academy of Sciences of the United States of America*, *111*(25), 9073–9078. https://doi.org/10.1073/pnas.1321679111

Myrow, P. (2003). Colors of sedimentary rocks. In *Sedimentology* (pp. 251–253). Springer Netherlands. https://doi.org/10.1007/978-1-4020-3609-5_52

Naito, Y., Costa, D. P., Adachi, T., Robinson, P. W., Peterson, S. H., Mitani, Y., & Takahashi, A. (2017). Oxygen minimum zone: An important oceanographic habitat for deep-diving northern elephant seals, *Mirounga angustirostris*. *Ecology and Evolution*, *7*(16), 6259–6270. https://doi.org/10.1002/ece3.3202

Norin, T., & Clark, T. D. (2017). Fish face a trade-off between ‘eating big’ for growth efficiency and ‘eating small’ to retain aerobic capacity. *Biology Letters*, *13*(9), 20170298. https://doi.org/10.1098/rsbl.2017.0298

Och, L. M., & Shields-Zhou, G. A. (2012). The Neoproterozoic oxygenation event: Environmental perturbations and biogeochemical cycling. In *Earth-Science Reviews* (Vol. 110, Issues 1–4, pp. 26–57). Elsevier. https://doi.org/10.1016/j.earscirev.2011.09.004

Oji, T., Ogaya, C., & Sato, T. (2003). Increase of shell-crushing predation recorded in fossil shell fragmentation. *Paleobiology*, *29*(4), 520–526. https://doi.org/10.1666/0094-8373(2003)029<0520:iospri>2.0.co;2

Passier, H. F., Middelburg, J. J., de Lange, G. J., & Böttcher, M. E. (1999). Modes of sapropel formation in the eastern Mediterranean: some constraints based on pyrite properties. *Marine Geology*, *153*(1–4), 199–219. https://doi.org/10.1016/S0025-3227(98)00081-4

Payne, J. L., & Heim, N. A. (2020). Body size, sampling completeness, and extinction risk in the marine fossil record. *Paleobiology*, *46*(1), 23–40. https://doi.org/10.1017/pab.2019.43

Payne, J. L., Heim, N. A., Knope, M. L., & McClain, C. R. (2014). Metabolic dominance of bivalves predates brachiopod diversity decline by more than 150 million years. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1783), 20133122. https://doi.org/10.1098/rspb.2013.3122

Payne, J. L., McClain, C. R., Boyer, A. G., Brown, J. H., Finnegan, S., Kowalewski, M., Krause, R. A., Lyons, S. K., McShea, D. W., Novack-Gottshall, P. M., Smith, F. A., Spaeth, P., Stempien, J. A., & Wang, S. C. (2011). The evolutionary consequences of oxygenic photosynthesis: a body size perspective. *Photosynthesis Research*, *107*(1), 37–57. https://doi.org/10.1007/s11120-010-9593-1

Planavsky, N. J., Reinhard, C. T., Wang, X., Thomson, D., McGoldrick, P., Rainbird, R. H., Johnson, T., Fischer, W. W., & Lyons, T. W. (2014a). Low Mid-Proterozoic atmospheric oxygen levels and the delayed rise of animals. *Science*, *346*(6209), 635–638. https://doi.org/10.1126/science.1258410

Planavsky, N. J., Reinhard, C. T., Wang, X., Thomson, D., McGoldrick, P., Rainbird, R. H., Johnson, T., Fischer, W. W., & Lyons, T. W. (2014b). Low mid-proterozoic atmospheric oxygen levels and the delayed rise of animals. In *Science* (Vol. 346, Issue 6209, pp. 635–638). American Association for the Advancement of Science. https://doi.org/10.1126/science.1258410

Raiswell, R., & Canfield, D. E. (1998). Sources of iron for pyrite formation in marine sediments. *American Journal of Science*, *298*(3), 219–245. https://doi.org/10.2475/ajs.298.3.219

Reinhard, C. T., Planavsky, N. J., Olson, S. L., Lyons, T. W., & Erwin, D. H. (2016). Earth's oxygen cycle and the evolution of animal life. *Proceedings of the National Academy of Sciences*, *113*(32), 8933–8938. https://doi.org/10.1073/pnas.1521544113

Rice, A. L., Billett, D. S. M., Fry, J., John, A. W. G., Lampitt, R. S., Mantoura, R. F. C., & Morris, R. J. (1986). Seasonal deposition of phytodetritus to the deep-sea floor. *Proceedings of the Royal Society of Edinburgh. Section B. Biological Sciences*, *88*, 265–279. https://doi.org/10.1017/s0269727000004590

Rickaby, R. E. M., & Eason Hubbard, M. R. (2019). Upper ocean oxygenation, evolution of RuBisCO and the Phanerozoic succession of phytoplankton. In *Free Radical Biology and Medicine* (Vol. 140, pp. 295–304). Elsevier Inc. https://doi.org/10.1016/j.freeradbiomed.2019.05.006

Rogers, A. D. (2015). Environmental Change in the Deep Ocean. In *Annual Review of Environment and Resources* (Vol. 40, pp. 1–38). Annual Reviews Inc. https://doi.org/10.1146/annurev-environ-102014-021415

Rohling, E. J. (1994). Review and new aspects concerning the formation of eastern Mediterranean sapropels. *Marine Geology*, *122*(1–2), 1–28. https://doi.org/10.1016/0025-3227(94)90202-X

Royer, D. L., Donnadieu, Y., Park, J., Kowalczyk, J., & Godderis, Y. (2014). Error analysis of CO2 and O2 estimates from the long-term geochemical model GEOCARBSULF. *American Journal of Science, 314*(9), 1259–1283. https://doi.org/10.2475/09.2014.01

Rubalcaba, J. G., Verberk, W. C. E. P., Hendriks, A. J., Saris, B., & Woods, H. A. (2020). Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences*, 202003292. https://doi.org/10.1073/pnas.2003292117

Rubalcaba, J. G., Verberk, W. C. E. P., Jan Hendriks, A., Saris, B., & Arthur Woods, H. (2020). Oxygen limitation may affect the temperature and size dependence of metabolism in aquatic ectotherms. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(50), 31963–31968. https://doi.org/10.1073/pnas.2003292117

SALAMON, M. A., BRACHANIEC, T., & GORZELAK, P. (2020). DUROPHAGOUS FISH PREDATION TRACES VERSUS TUMBLING-INDUCED SHELL DAMAGE—A PALEOBIOLOGICAL PERSPECTIVE. *PALAIOS*, *35*(1), 37–47. https://doi.org/10.2110/palo.2019.091

Saltzman, M. R. (2005). Phosphorus, nitrogen, and the redox evolution of the Paleozoic oceans. *Geology*, *33*(7), 573–576. https://doi.org/10.1130/G21535.1

Scott, A. C., & Glasspool, I. J. (2006). The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(29), 10861–10865. https://doi.org/10.1073/pnas.0604090103

Seibel, B. A. (2011). Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *Journal of Experimental Biology*, *214*(2), 326–336. https://doi.org/10.1242/jeb.049171

Seibel, B. A., & Deutsch, C. (2020). Oxygen supply capacity in animals evolves to meet maximum demand at the current oxygen partial pressure regardless of size or temperature. *Journal of Experimental Biology*, *223*(12). https://doi.org/10.1242/jeb.210492

Sepkoski, J. J., & Sheehan, P. M. (1983). Diversification, faunal change, and community replacement during the Ordovician radiations. *Biotic Interactions in Recent and Fossil Benthic Communities*, 673–717. https://doi.org/10.1007/978-1-4757-0740-3_14

Sepkoski, J. John. (1981). A factor analytic description of the Phanerozoic marine fossil record. *Paleobiology*, *7*(1), 36–53. https://doi.org/10.1017/s0094837300003778

Sigwart, J. D., Wicksten, M. K., Jackson, M. G., & Herrera, S. (2019). Deep-sea video technology tracks a monoplacophoran to the end of its trail (Mollusca, Tryblidia). *Marine Biodiversity*, *49*(2), 825–832. https://doi.org/10.1007/s12526-018-0860-2

Smith, F. A., Betancourt, J. L., & Brown, J. H. (1995). Evolution of body size in the woodrat over the past 25,000 years of climate change. *Science*, *270*(5244), 2012–2014. https://doi.org/10.1126/science.270.5244.2012

Smith, F. A., Payne, J. L., Heim, N. A., Balk, M. A., Finnegan, S., Kowalewski, M., Lyons, S. K., McClain, C. R., McShea, D. W., Novack-Gottshall, P. M., Anich, P. S., & Wang, S. C. (2016). Body Size Evolution Across the Geozoic. *Annual Review of Earth and Planetary Sciences*, *44*(1), 523–553. https://doi.org/10.1146/annurev-earth-060115-012147

Smith, K. E., & Thatje, S. (2012). The Secret to Successful Deep-Sea Invasion: Does Low Temperature Hold the Key? *PLoS ONE*, *7*(12), e51219. https://doi.org/10.1371/journal.pone.0051219

Smith, K. L., Ruhl, H. A., Bett, B. J., Billett, D. S. M., Lampitt, R. S., & Kaufmann, R. S. (2009). Climate, carbon cycling, and deep-ocean ecosystems. In *Proceedings of the National Academy of Sciences of the United States of America* (Vol. 106, Issue 46, pp. 19211–19218). National Academy of Sciences. https://doi.org/10.1073/pnas.0908322106

Smith, Kenneth L., Ruhl, H. A., Huffard, C. L., Messié, M., & Kahru, M. (2018). Episodic organic carbon fluxes from surface ocean to abyssal depths during long-term monitoring in NE Pacific. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(48), 12235–12240. https://doi.org/10.1073/pnas.1814559115

Somero, G. N. (1992). Adaptations to high hydrostatic pressure. In *Annual Review of Physiology* (Vol. 54, pp. 557–577). Annu Rev Physiol. https://doi.org/10.1146/annurev.ph.54.030192.003013

Song, H., Jiang, G., Poulton, S. W., Wignall, P. B., Tong, J., Song, H., An, Z., Chu, D., Tian, L., She, Z., & Wang, C. (2017). The onset of widespread marine red beds and the evolution of ferruginous oceans. *Nature Communications*, *8*(1), 399. https://doi.org/10.1038/s41467-017-00502-x

Sperling, E. A., Frieder, C. A., Raman, A. V., Girguis, P. R., Levin, L. A., & Knoll, A. H. (2013). Oxygen, ecology, and the Cambrian radiation of animals. *Proceedings of the National Academy of Sciences*, *110*(33), 13446–13451. https://doi.org/10.1073/pnas.1312778110

Sperling, Erik A., Knoll, A. H., & Girguis, P. R. (2015). The Ecological Physiology of Earth's Second Oxygen Revolution. *Annual Review of Ecology, Evolution, and Systematics*, *46*(1), 215–235. https://doi.org/10.1146/annurev-ecolsys-110512-135808

Stanley, S. M. (2020). Evidence that more than a third of Paleozoic articulate brachiopod genera (Strophomenata) lived infaunally. *Paleobiology*, *46*(3), 405–433. https://doi.org/10.1017/pab.2020.29

Sturdivant, S. K., Díaz, R. J., & Cutter, G. R. (2012). Bioturbation in a Declining Oxygen Environment, in situ Observations from Wormcam. *PLoS ONE*, *7*(4), e34539. https://doi.org/10.1371/journal.pone.0034539

Thayer, C. W. (1979). Biological bulldozers and the evolution of marine benthic communities. *Science*, *203*(4379), 458–461. https://doi.org/10.1126/science.203.4379.458

Thayer, C. W. (1983). *Sediment-Mediated Biological Disturbance and the Evolution of Marine Benthos* (pp. 479–625). https://doi.org/10.1007/978-1-4757-0740-3_11

Turner, J. T. (2015). Zooplankton fecal pellets, marine snow, phytodetritus and the ocean's biological pump. In *Progress in Oceanography* (Vol. 130, pp. 205–248). Elsevier Ltd.

https://doi.org/10.1016/j.pocean.2014.08.005

van de Velde, S., & Meysman, F. J. R. (2016). The Influence of Bioturbation on Iron and Sulphur Cycling in Marine Sediments: A Model Analysis. *Aquatic Geochemistry*, *22*(5–6), 469–504. https://doi.org/10.1007/s10498-016-9301-7

Van De Velde, S., Mills, B. J. W., Meysman, F. J. R., Lenton, T. M., & Poulton, S. W. (2018). Early Palaeozoic ocean anoxia and global warming driven by the evolution of shallow burrowing. *Nature Communications*, *9*(1). https://doi.org/10.1038/s41467-018-04973-4

Verberk, W. C. E. P., Bilton, D. T., Calosi, P., & Spicer, J. I. (2011). Oxygen supply in aquatic ectotherms: Partial pressure and solubility together explain biodiversity and size patterns. *Ecology*, *92*(8), 1565–1572. https://doi.org/10.1890/10-2369.1

Vermeij, G. J. (1983). Shell-breaking predation through time. *Biotic Interactions in Recent and Fossil Benthic Communities*, 649–669. https://doi.org/10.1007/978-1-4757-0740-3_13

Vermeij, Geerat J. (1977a). The mesozoic marine revolution: Evidence from snails, predators and grazers. *Paleobiology*, *3*(3), 245–258. https://doi.org/10.1017/S0094837300005352

Vermeij, Geerat J. (1977b). The Mesozoic marine revolution: evidence from snails, predators and grazers. *Paleobiology*, *3*(03), 245–258. https://doi.org/10.1017/S0094837300005352

Vermeij, Geerat J. (2013). On Escalation. *Annual Review of Earth and Planetary Sciences*, *41*(1), 1–19. https://doi.org/10.1146/annurev-earth-050212-124123

Vermeij, Geerat J. (2016). Gigantism and Its Implications for the History of Life. *PLOS ONE*, *11*(1), e0146092. https://doi.org/10.1371/journal.pone.0146092

Wallace, M. W., Hood, A. vS., Shuster, A., Greig, A., Planavsky, N. J., & Reed, C. P. (2017). Oxygenation history of the Neoproterozoic to early Phanerozoic and the rise of land plants. *Earth and Planetary Science Letters*, *466*, 12–19. https://doi.org/10.1016/j.epsl.2017.02.046

Wang, K., Shen, Y., Yang, Y., Gan, X., Liu, G., Hu, K., Li, Y., Gao, Z., Zhu, L., Yan, G., He, L., Shan, X., Yang, L., Lu, S., Zeng, H., Pan, X., Liu, C., Yuan, Y., Feng, C., … He, S. (2019). Morphology and genome of a snailfish from the Mariana Trench provide insights into deep-sea adaptation. *Nature Ecology and Evolution*, *3*(5), 823–833. https://doi.org/10.1038/s41559-019-0864-8

Westrich, J. T., & Berner, R. A. (1984). The role of sedimentary organic matter in bacterial sulfate reduction: The G model tested1. *Limnology and Oceanography*, *29*(2), 236–249. https://doi.org/10.4319/lo.1984.29.2.0236

Wilkin, R. T., Barnes, H. L., & Brantley, S. L. (1996). The size distribution of framboidal pyrite in modern sediments: An indicator of redox conditions. Geochimica et Cosmochimica Acta, 60(20), 3897–3912. https://doi.org/10.1016/0016-7037(96)00209-8

Zezina, O. N. (1994). Deep-sea brachiopods. Their peculiarities in morphology and evolution. *Sarsia*, *79*(1), 59–64. https://doi.org/10.1080/00364827.1994.10413548