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Mechanisms of Devonian ocean anoxic events: insights from Earth system modelling

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by Justin Gérard

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If I have seen further, it is by standing on the shoulders of giants.

Isaac Newton

Surround yourself with people who make you happy. People who make you laugh, who help you when you're in need. People who genuinely care. They are the ones worth keeping in your life. Everyone else is just passing through.

Karl Marx

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Abstract

Recurrent events of severe ocean deoxygenation during the Devonian Period represent major disruptions of the marine environment, yet many mysteries still surround them. To address specific aspects of these events, we use the Earth system model of intermediate complexity cGENIE to investigate the controls on ocean oxygenation through a series of targeted numerical experiments. Our results highlight the dominant role of continental configuration in shaping ocean circulation and modulating the response of oxygenation to other environmental and climatic forcings. We further show that astronomical forcing can strongly influence ocean oxygenation through its control on continental nutrient weathering fluxes and biological productivity, producing substantial spatially contrasted responses, and intervals of eccentricity maxima associated with increased anoxia. Finally, model–data comparisons for the Kellwasser events indicate that increased nutrient availability can adequately reproduce the extent and seafloor fraction of anoxia, providing quantitative benchmarks against which different mechanisms and hypotheses can be tested.

Contents

Contents	vii
List of abbreviations	ix
1 Introduction	1
1.1 Devonian Period and OAEs	3
1.2 Modern tools to understand past climate	11
1.3 Thesis objectives, method, and outline	17
2 Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing	23
2.1 Introduction	23
2.2 Methods	25
2.3 Results	29
2.4 Discussion	43
2.5 Conclusions	47
3 Spatially contrasted response of Devonian anoxia to astronomical forcing	51
3.1 Introduction	51
3.2 Methods	52
3.3 Results	58
3.4 Discussion	65
3.5 Conclusions	70
4 The Kellwasser Crisis: How to trigger global anoxia?	73
4.1 Introduction	73

★ | Contents

4.2	Methods	74
4.3	Comparing model simulation with geological records	81
4.4	Reconstruction of LKE and UKE	84
5	Conclusions	87
5.1	Research results	87
5.2	Perspective	90
A	Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale	93
A.1	Introduction	93
A.2	Methods	96
A.3	Results	98
A.4	Discussion and conclusions	109
B	Appendix to Chapter 2	113
B.1	Limit cycle in Scot420M	113
C	Appendix to Chapter 3	115
C.1	Background state and ocean circulation	115
C.2	Defining regions	116
D	Appendix to Chapter 4	119
D.1	Data locations: redox evidence and lithology	119
D.2	Second scoring method	121
E	List of publications related to the thesis	125
	Bibliography	127

List of abbreviations

Devonian and ocean anoxia elements

OAE	Ocean Anoxic Event
F-F	Frasnian-Famenian
D-C	Devonian-Carboniferous
LKE	Lower Kellwasser Event
UKE	Upper Kellwasser Event
POM	Particulate Organic Matter
OMZ	Oxygen Minimum Zone

Model hierarchy

ESM	Earth System Model
GCM	General Circulation Model
EMIC	Earth system Model of Intermediate Complexity

Others

AMOC	Atlantic Meridional Overturning Circulation
MOC	Meridional Overturning Circulation
THC	Thermohaline Circulation
NADW	North Atlantic Deep Water
RCP	Representative Concentration Pathway
CMIP	Coupled Model Intercomparison Project

★ | Contents

PAL Preindustrial Atmospheric Level

1

Introduction

Humanity has long tried to understand the natural world and the laws that govern it. Among the most central scientific questions is that of life and its evolution: how did biodiversity evolve, from simple unicellular organisms to the remarkable diversity and complexity of life we observe today?

The evolution of life cannot be understood independently of the environmental conditions under which it developed (Knoll, 2015). Throughout Earth's history, biological diversification, ecological crises, and extinction events have been closely linked to changes in climate, ocean chemistry, and atmospheric composition (Lyons et al., 2014; Bond and Grasby, 2017). Geological records, such as rocks, preserve evidence of these long-term interactions, offering a unique window into how environmental constraints and disturbances have shaped life over hundreds of millions of years (Myr). These records have revealed several intervals of major biological turnover, such as the Permian-Triassic extinction event, which took place 252 million years ago (Ma) and during which ~90 % of marine species disappeared (Chen and Benton, 2012) (see Fig. 1.1). As oxygen (O_2) is essential to all complex marine organisms that rely on aerobic respiration, the O_2 content of the ocean is believed to have played a major role in shaping marine biodiversity throughout the Phanerozoic Eon (the last 539 Myr) (Semenza, 2007). Fossil evidence indicates a strong link between reduced oceanic dissolved O_2 concentration ($[O_2]$) and biodiversity loss, with several major extinction events associated with episodes of severe

ocean deoxygenation, often referred to as ocean anoxic events (OAEs) (Jenkyns, 2010).

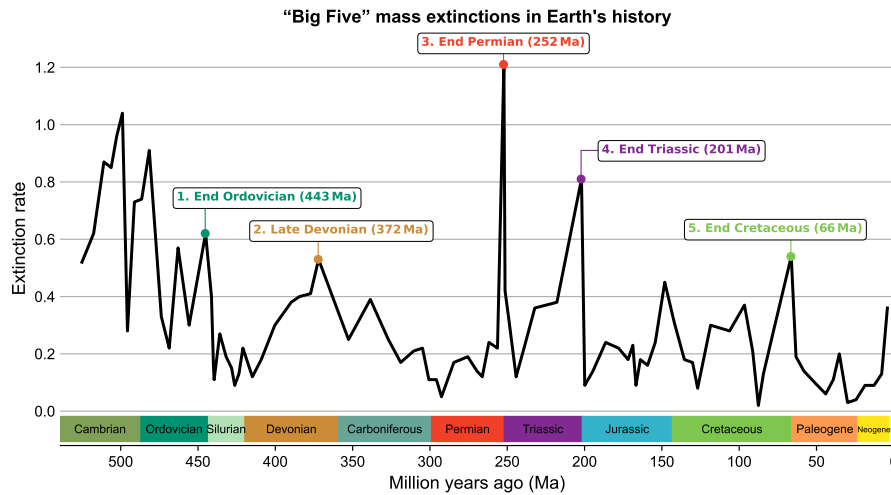


Fig. 1.1 Time evolution of marine species extinction rates throughout the Phanerozoic Eon (last 539 million years). An extinction event is defined as a rapid, large-scale decrease in the diversity and abundance of life on Earth (Whiteside and Grice, 2016). Several events of exceptionally high extinction intensity are visible, corresponding to major mass extinction episodes, including the end-Ordovician, Late Devonian, end-Permian, end-Triassic, and end-Cretaceous events. These events are often collectively referred to as the “Big Five”, although this classification has been increasingly questioned, and the broader terms major or first-order mass extinctions are generally preferred. This figure is reproduced from Stockey et al. (2021), based on Kocsis et al. (2019).

Today, human activities are profoundly altering the Earth’s climate (IPCC, 2021). The large-scale combustion of fossil fuels has led to a rapid increase in atmospheric greenhouse gas concentrations, driving global warming at a rate that challenges the adaptive capacity of many ecosystems. As a consequence, the ocean has lost around 2 % of its O_2 content over the last five decades (Schmidtko et al., 2017; Breitburg et al., 2018). These variations in global temperature and ocean $[O_2]$ are accompanied by widespread biodiversity loss, and could culminate in a mass extinction similar to those in Earth’s past (Penn and Deutsch, 2022).

The investigation of past climates thus serves two closely related purposes: improving our understanding of the environmental conditions that controlled the evolution of life, and providing a longer perspective on current environmental change. Geological records document past changes in climate across a

wide range of timescales, from abrupt events to long-term trends. Studying these past changes helps clarify how Earth's natural processes may respond to the rapid, human-driven warming observed today, thereby improving our assessment of plausible future trajectories of the climate system across different timescales.

In this context, the general objective of this thesis is to contribute to a better understanding of the mechanisms and dynamics driving OAEs using numerical modelling. At a more specific level, it focuses on the Devonian Period, with particular emphasis on the role of astronomical forcing in modulating ocean oxygenation. Section 1.1 introduces the Devonian Period and its recurrent OAEs. Section 1.2 presents the modelling tools used to study past climate and ocean conditions. Section 1.3 defines the specific objectives of this thesis.

1.1 Devonian Period and OAEs

1.1.1 The Devonian Period

The Devonian Period, spanning from 419.62 to 358.86 Ma, is the fourth period of the Phanerozoic Eon and the Paleozoic Era. It was first defined in the 19th century by Sedgwick and Murchison (1839) based on a rock section exposed in North Devon, South West England, from which the period takes its name. The Devonian lies between the Silurian and the Carboniferous, two other major periods of the Paleozoic. The Devonian is subdivided into three series: the Lower, Middle, and Upper Devonian, with the Lower and Upper series also commonly referred to as the Early and Late Devonian, respectively. The Early Devonian includes the Lochkovian, Pragian, and Emsian stages; the Middle Devonian includes the Eifelian and Givetian stages; and the Late Devonian is divided into the Frasnian and Famennian stages (Becker et al., 2020).

Over its ~60 Myr duration, the Devonian Period was marked by major evolutionary events and pronounced climatic changes, expressed through both long-term trends and abrupt changes. One of its most influential biological developments is the progressive colonization of terrestrial environments by plants. Early Devonian vegetation developed increasingly complex rooting systems, culminating in the establishment of the first primitive forests during

the Middle Devonian. This transition profoundly modified terrestrial ecosystems, with strong consequences for climate, weathering, and ocean chemistry (Algeo and Scheckler, 1998; Liu et al., 2025). The Devonian is also characterized by a peak in carbonate (CO_3) production, marked by extensive reef development, and records the greatest marine faunal diversity of the Paleozoic (Becker et al., 2020). The rapid diversification of jaw-bearing fishes during this period has led to the Devonian being nicknamed “the age of fish” (Dahl et al., 2010). Yet, this biological richness was punctuated by major crises, including two first-order mass extinctions occurring at the Frasnian–Famennian (F–F) and Devonian–Carboniferous (D–C) boundaries, commonly known as the Kellwasser and Hangenberg events, respectively (Becker et al., 2020).

The Devonian is also widely recognized as a warmer-than-present period, although the magnitude and persistence of these warm conditions are actively debated. According to the classical view, much of the Devonian was dominated by greenhouse conditions (Joachimski et al., 2009), with estimated atmospheric carbon dioxide concentrations ($[\text{CO}_2]$) up to ten times those of the present day (Berner, 2006). Toward its end, however, the Devonian witnessed substantial climatic cooling, associated with a decline in atmospheric $[\text{CO}_2]$ to near preindustrial levels, possibly driven by the proliferation of land forests, and culminating in glaciation at the D–C transition (Berner, 2006). In contrast to this classical view, more recent estimates propose substantially lower atmospheric $[\text{CO}_2]$ throughout the Devonian (Chen et al., 2021), with values as low as ~ 500 parts per million (ppm) and icehouse conditions persisting over much of the period (Dahl et al., 2022).

Because it corresponds to a time interval deep in Earth’s past, the Devonian continental configuration differs markedly from that of the present day. Figure 1.2 illustrates the topography of the Middle Devonian based on the continental reconstruction of Scotese and Wright (2018). Devonian palaeogeography was dominated by the supercontinent Gondwana in the Southern Hemisphere, comprising present-day South America, Africa, Arabia, Madagascar, India, Australia, and Antarctica; the relatively small continent of Siberia to the north; and Laurussia, which included North America, Greenland, and parts of Europe. Most continents and shallow shelves were clustered within the Southern Hemisphere, resulting in the development of a vast open ocean, often referred to as the Panthalassa or Proto-Pacific Ocean (Becker et al., 2020). The continental reconstructions of Scotese and Wright (2018) are among the most widely used. Numerous other palaeogeographic models exist (Torsvik and

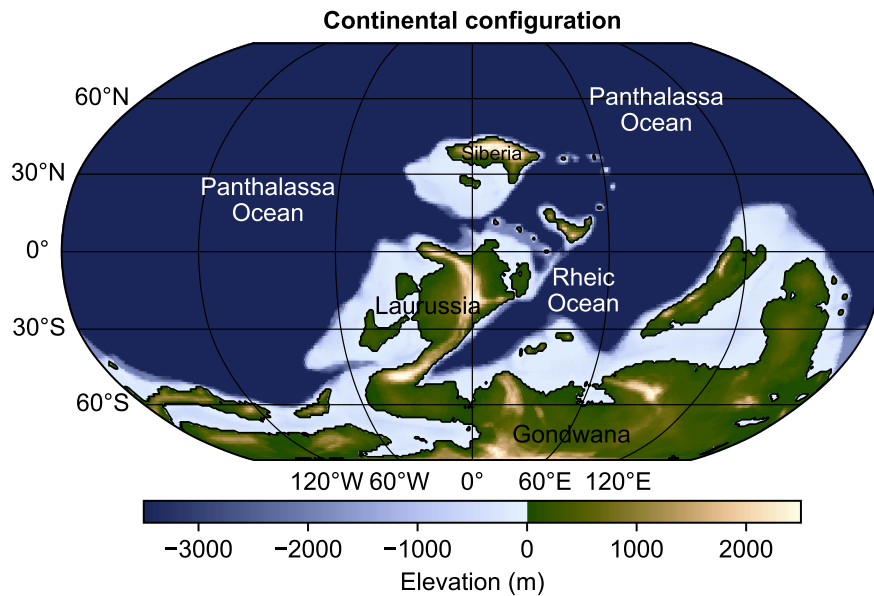


Fig. 1.2 *Continental configuration of the Middle Devonian (390.5 Ma).* Topography of the Middle Devonian expressed as an elevation (m) from the sea level according to the reconstructions of Scotese and Wright (2018). Negative values (blue) represent the ocean and positive values (green) the land masses.

Cocks, 2013; Blakey, 2016; V  rard, 2019a; Merdith et al., 2021), derived from different methodological approaches and yield often substantially different continental configurations.

Overall, the Devonian represents a time of profound change, markedly different from the present. Reconstructing its environmental conditions is inherently challenging, as illustrated by the substantial uncertainties that persist in palaeogeographic reconstructions and estimates of atmospheric [CO₂]. As a result, the Devonian holds many mysteries, which motivate active research!

1.1.2 Recurrent OAEs

The Kellwasser and Hangenberg crises represent the most severe extinction events of the Devonian, but they are not isolated occurrences. Figure 1.3 summarizes the Devonian stages together with the numerous extinction events

that have been identified throughout the period. Although the Kellwasser and Hangenberg events stand out as the only first-order mass extinctions, the Devonian records include many other extinction pulses of variable intensity, ranging from second-order events to more minor disturbances, here classified at level 5 (Fig. 1.3). Notably, these extinction events are unevenly distributed through time, with frequency and intensity both markedly higher during the Middle and Late Devonian than during the Early Devonian.

Over recent decades, ocean anoxia has been generally established as the primary kill mechanism associated with extinction events (Johnson et al., 1985; Jenkyns, 2010; Kaiser et al., 2016). Nevertheless, the causal relationship between anoxia and extinction during the Devonian is complex and not systematically apparent in geological records (Carmichael et al., 2019; Becker et al., 2020). This complexity is particularly evident temporally, as shown in Fig. 1.3, where some extinction events closely coincide with evidence for anoxia, whereas others do not. In addition, the timing of the anoxic onset can vary spatially, with multiple diachronous anoxic episodes combining to produce an apparently synchronous, global signal (Hedhli et al., 2023). While such observations are often used to question causality, they may instead reflect the complex and heterogeneous response of marine ecosystems to anoxia during extinction events (Wang et al., 2025).

Beyond anoxia, several alternative potential kill mechanisms have been proposed, including climatic cooling (Song et al., 2017a; Pier et al., 2021) and warming (Fields et al., 2020), ocean acidification (Ernst et al., 2020), sea level changes (Bond and Wignall, 2008), and methylmercury poisoning (Rakociński et al., 2020). Despite this plurality of hypotheses, evidence for ocean anoxia has been documented across all Devonian extinction events of first and second orders (see Fig. 1.3) and anoxia remains the most widely invoked driver for biodiversity loss during this period (Zhang et al., 2020a; Sahoo et al., 2023; Smart et al., 2023; Zheng et al., 2023; Wang et al., 2025).

Therefore, it is essential to understand the processes that determine oceanic $[O_2]$, and thus the mechanisms controlling the uptake and release of O_2 . In the ocean interior, $[O_2]$ is governed by two main components: the biological pump and physical transport (Peña et al., 2010). The biological pump refers to the set of processes that transfer organic carbon (C_{org}) from the surface to the deep ocean. The ocean acts as a major carbon (C) reservoir by absorbing atmospheric CO_2 , a fraction of which is fixed into C_{org} through photosyn-

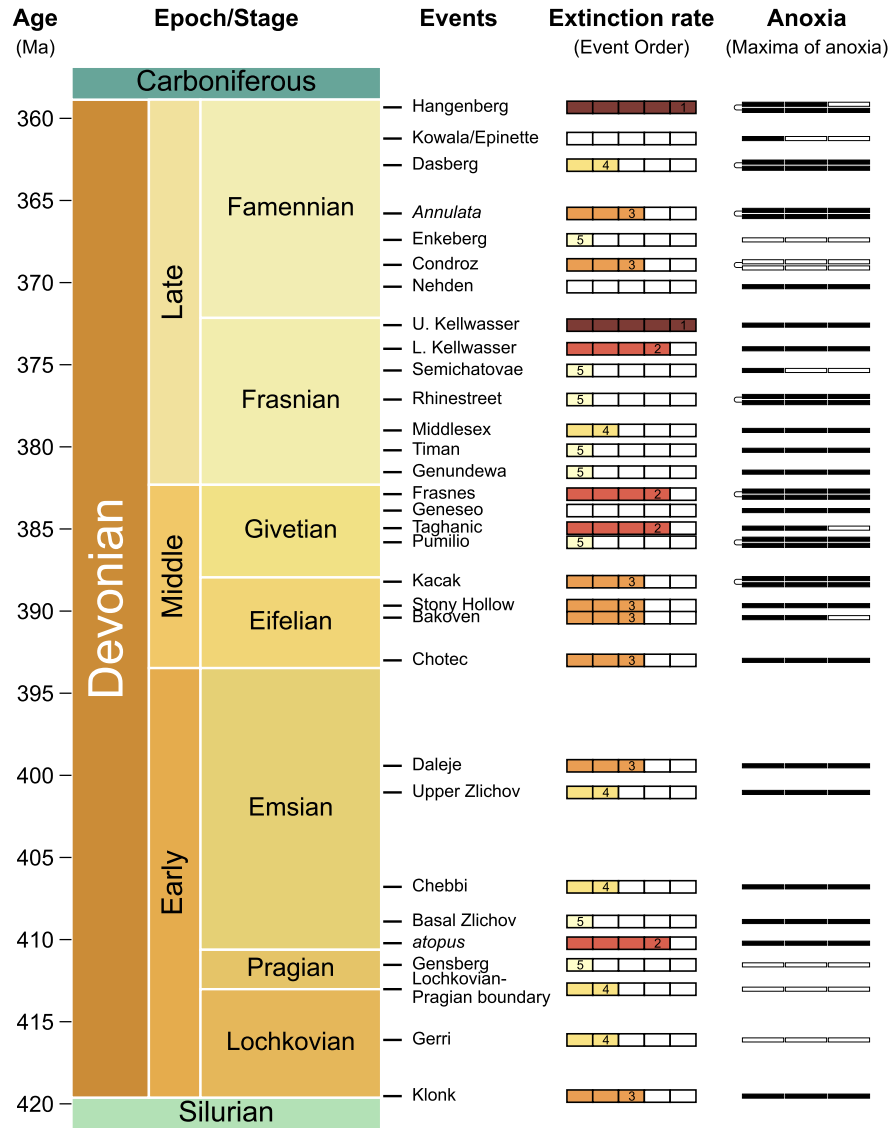


Fig. 1.3 Devonian time scale and extinction events. Temporal framework of the Devonian based on numerical ages from ICS (2025), showing the numerous events that occurred throughout this period. The magnitude of extinction associated with each event is indicated (Brett et al., 2020), together with the maxima of anoxic sedimentation (Becker et al., 2016; Becker et al., 2020). Estimates of the duration of the Devonian OAEs range between 10^4 and 10^6 years (Kabanov et al., 2023). For some events, “doublets” of black shale deposition are recognized (e.g., Hangenberg, Dasberg, and Condroz) and are indicated with the ◡ symbol. This figure is adapted from the work of Jarno Huygh.

thesis, referred to as net primary productivity. Although most of this C_{org} is ultimately respired back into inorganic C, a portion of organic matter (often called export production) is transported to depth (Yamaguchi et al., 2024). When this export production sinks, O_2 is consumed by microbial processes to remineralise organic matter. The intensity of this O_2 consumption is directly tied to net primary productivity, which scales with the availability of essential nutrients, notably phosphate (PO_4), often considered as the ultimate limiting nutrient on geological timescales (Tyrrell, 1999). Nutrient enrichment can therefore enhance export production and amplify O_2 depletion within the water column. Through physical transport, O_2 is supplied to the ocean interior. The atmosphere holds an estimated 10^{19} mol of O_2 , roughly two orders of magnitude more than the 10^{17} mol dissolved in seawater (Duursma and Boisson, 1994; Schmidtke et al., 2017). The dissolution of atmospheric O_2 into surface waters, together with the O_2 produced by net primary productivity, maintain a well-oxygenated surface ocean. The process of transporting these oxygen-rich waters to depth through mixing and large-scale ocean circulation is commonly referred to as ventilation. The biological pump, acting as an O_2 sink, together with the physical transport, acting as an O_2 source, constitute the primary controls on $[O_2]$ in the ocean interior (see Fig. 1.4). Consequently, any mechanism that alters the efficiency of either component or the balance between them has the potential to strongly influence the global ocean $[O_2]$.

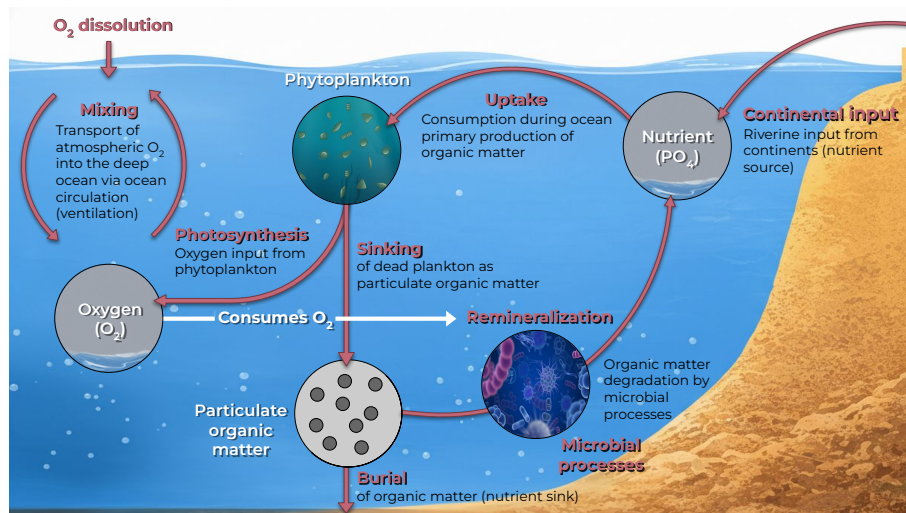


Fig. 1.4 Schematic of the main processes governing O_2 in the ocean interior. Simplified illustration of the physical transport and biological pump, with focus on O_2 . Red elements represent processes, while white elements denote the different reservoirs.

This diversity of processes capable of altering the biological pump or physical ventilation has motivated the formulation of multiple competing hypotheses. However, the mechanisms responsible for triggering Devonian OAEs are debated and, to some extent, speculative. One proposed mechanism involves the evolution and expansion of terrestrial plants, together with the development of increasingly complex root systems. The resulting intensification of chemical weathering and soil formation likely enhanced riverine phosphorus (P) delivery to the oceans. This over-enrichment of water with nutrients, commonly referred to as eutrophication, would have stimulated marine primary productivity, hence O₂ consumption (Algeo and Scheckler, 1998; Smart et al., 2023). Large-scale volcanic activity has also been suggested as a potential trigger of OAEs. Volcanic eruptions may have influenced climate and atmospheric composition through greenhouse gas emissions, while simultaneously supplying nutrients and trace metals that could have further enhanced the biological pump (Keith, 1982; Paschall et al., 2019; Racki, 2020; Kabanov et al., 2023). Variations in ocean circulation represent another possible mechanism. Changes in circulation can modulate O₂ distribution by altering ventilation efficiency and upwelling patterns, thereby influencing both the supply of O₂ to the ocean interior and the delivery of nutrients to surface waters (Caplan and Bustin, 1999; Chen et al., 2013).

More recently, evidence also points toward the role of astronomical forcing in modulating Devonian OAEs. Astronomical, orbital, or Milankovitch forcing refers to the quasi-periodic variations in Earth's orbital parameters, namely eccentricity, obliquity, and the longitude of perihelion (precession) (see Fig. 1.5). Because these variations arise from gravitational interactions among Solar System bodies, and because the Solar System dynamics is inherently chaotic, the exact astronomical configuration during the Devonian cannot be reconstructed precisely (Laskar et al., 2011). Reliable astronomical solutions for precession, obliquity, and their phase relationships are generally considered to extend no further than ~50 Myr into the past (Laskar et al., 2004). Nevertheless, it is possible to estimate the characteristic periods of each astronomical parameter. For the Devonian, eccentricity periods are thought to have been broadly similar to those of the present day, with dominant cycles near 100 thousand years (kyr), 405 kyr, and 2.4 Myr. Obliquity likely exhibited shorter cycles than today, approximately 30 kyr, 37 kyr, and 1.2 Myr, while precession is estimated to have varied with cycles of about 16 and 19 kyr. The mean obliquity is also believed to have been lower than at present, around 22.2° compared to 23.3°

today (Farhat et al., 2022). While these values represent plausible estimates for the Devonian, the stability of some long-period cycles, such as the 405 kyr and 2.4 Myr eccentricity cycles and the 1.2 Myr obliquity cycle, is not systematically reproduced in all astronomical solutions (Zeebe and Lantink, 2024).

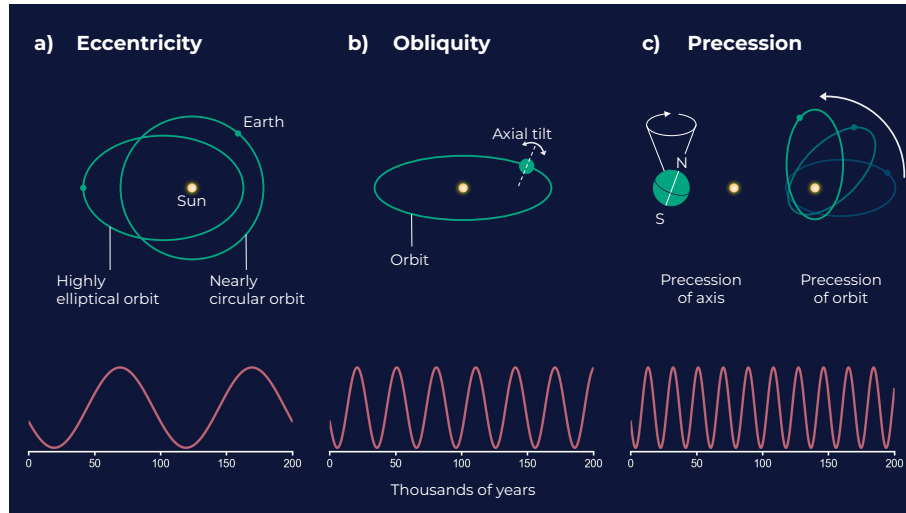


Fig. 1.5 Conceptual representation of the astronomical parameters. (a) Eccentricity (e) characterizes the elliptical nature of Earth's orbit around the Sun and influences the total amount of annual insolation it receives. (b) Obliquity (ε) describes the tilt of Earth's rotational axis and controls the latitudinal distribution of annual mean insolation. (c) The revolution of the longitude of perihelion (ϖ), referred to as climatic precession (hereafter simply precession), results from the combined effects of axial and orbital precession and influences the seasonal distribution of insolation throughout the year. This influence of precession on insolation is modulated by the eccentricity. Typical Devonian cycles for eccentricity (100 kyr), obliquity (30 kyr), and precession (19 kyr) are indicated by the red lines. This figure is adapted from Maslin (2016).

Astronomical forcing has been proposed as a mechanism pacing the recurrence of OAEs. For instance, De Vleeschouwer et al. (2013) showed that *Annulata*, Dasberg, and Hangenberg OAEs are spaced ~ 2.4 Myr apart, pointing towards a role of eccentricity in the timing of these events. However, substantial uncertainties remain regarding the phase relationship between astronomical forcing and the initiation of Devonian OAEs. Several studies propose that anoxic intervals tend to occur shortly after minima in the 2.4 Myr eccentricity cycle (De Vleeschouwer et al., 2017; Da Silva et al., 2020; Wichern et al., 2024). During prolonged eccentricity minima, the weak amplitude of precession-driven seasonality would reduce continental runoff and favour pro-

gressive nutrient accumulation on the continents. As eccentricity subsequently increases, the strengthening of precession forcing would enhance seasonal contrasts and intensify continental runoff. The resulting pulse of nutrient input may ultimately lead to eutrophication and anoxia. This sequence of processes has been described as the “nutrient-gun” hypothesis (De Vleeschouwer et al., 2014). In contrast, other studies suggest that OAEs were associated with strong obliquity and eccentricity (Ma et al., 2022; Huygh et al., 2025). Under such astronomical configurations, enhanced seasonal contrasts would strengthen hydrological cycling and increase nutrient delivery to the oceans, potentially accompanied by sea-level rise. These conditions would also favour intensified primary productivity and subsequent O₂ consumption in the ocean interior. Taken together, these differing interpretations highlight that multiple explanations and mechanistic relationships coexist within a broader hypothesis for the onset of anoxia.

The plurality of hypotheses suggests also that Devonian OAEs were likely not driven by a single mechanism. Rather, their onset and development most probably resulted from the combined influence of multiple physical and biogeochemical processes, whose relative importance may have shifted through time and from event to event. In this context, finding the interplay of mechanisms preconditioning the ocean to anoxia is likely a key element in understanding these events. Even if the triggers differ, they could converge toward similar consequences: enhanced terrestrial nutrient input or intensified marine upwelling (Smart et al., 2023). Such convergence toward common pathways provides a coherent framework for investigating how climate forcing may have repeatedly pushed the Devonian ocean toward anoxic conditions.

1.2 Modern tools to understand past climate

The Devonian occurred ~400 Ma, raising a fundamental question: how can scientists reconstruct environmental conditions, biological events, and related mechanisms so far back in time? Investigating the deep past becomes increasingly challenging as we move further away from the present, as the direct archives available for recent climate reconstructions become progressively scarce or absent. Archives like tree rings extend only a few millennia into the past, and the longest ice core records only reach back a few million years

(Fischer et al., 2013). Beyond these limits, the primary archive that remains is rock. Consequently, the study of rocks and the proxies they contain constitutes our primary window into the Devonian. Over the past decades, climate modelling has increasingly complemented these geological records. Together, proxy records derived from rocks and numerical climate models constitute the two principal tools for investigating the Devonian and, more broadly, the deep geological past, each offering a distinct and complementary perspective on the same system (see Fig. 1.6).

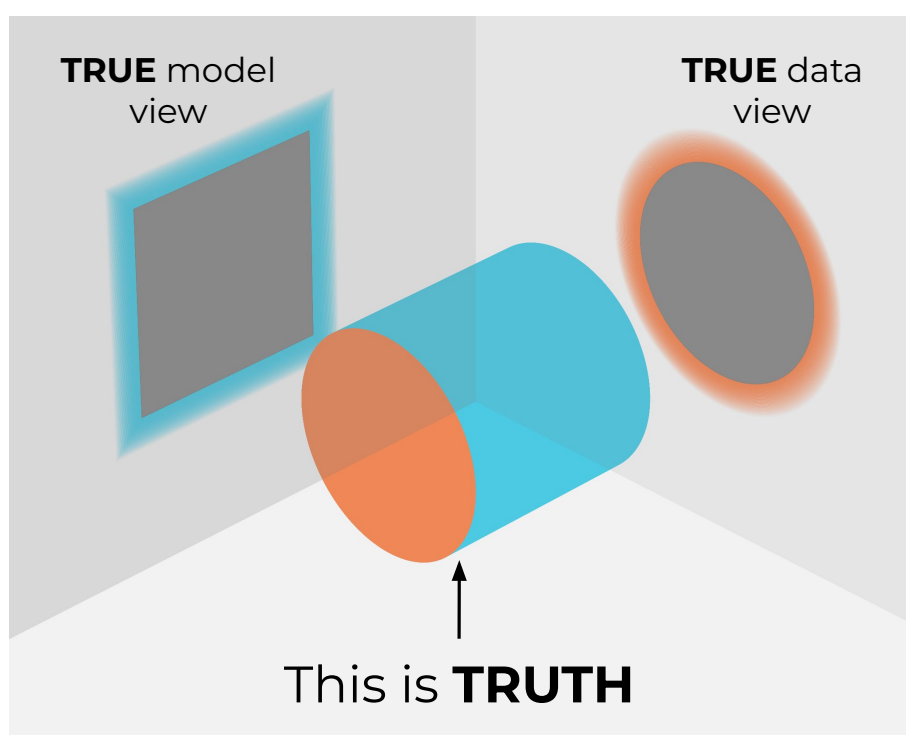


Fig. 1.6 Schematic view of model and data perspective. Graphical illustration of the complementary perspective of modelling and proxy records approaches. It exemplifies how an underlying truth (cylinder) can yield contrasting yet complementary interpretations (square and circle), both valid, depending on the perspective (model and data).

1.2.1 Geological records

Rocks provide indirect evidence of past environmental conditions through the geochemical, sedimentological, and paleontological signals they preserve. Estimating the duration of the Devonian or the precise timing of an extinction

event is no simple task. It requires several complementary approaches to constrain the relative or absolute age of geological records. It is, for instance, possible to use fossils of different species to assess the age of rock strata (biostratigraphy). The appearance, disappearance, and evolutionary succession of species are used to define zonations that subdivide the geological record into chronologically ordered intervals. For the Devonian, such zonations are typically established using the fossil record of conodonts, ammonoids, entomozoid ostracods, chitinozoans, and dactyloconarids. Additional constraints can be obtained from physical and chemical stratigraphic approaches, such as radiometric dating based on the decay rate of radioactive isotopes (e.g., uranium-lead), magnetostratigraphy based on magnetic reversals preserved in sediments, and variations in the isotopic composition of elements such as C or O₂ to correlate stratigraphic intervals (Becker et al., 2020).

Cyclostratigraphy is another technique to measure time in geological records. It identifies periodic patterns in sedimentary sequences that reflect the influence of astronomical cycles on the climate system. These rhythmic sedimentary successions can then be used to refine relative age models and estimate the duration of geological intervals. When such cycles can be confidently identified and calibrated, cyclostratigraphy is one of the most precise tools for constraining the duration and timing of geological intervals. Nevertheless, despite the numerous methods and scientific advances, establishing an accurate chronology for the Devonian remains extremely challenging. For instance, ~35 years ago, the Devonian was thought to span only ~46 Myr (408.5 to 362.5 Ma), illustrating how geological timescale estimates can shift substantially as new data and methods emerge (Becker et al., 2020).

In addition to temporal information, the geological record also preserves evidence of biological crises, ocean anoxia, and perturbations of global biogeochemical cycles. Many Devonian extinction events are stratigraphically associated with the deposition of organic-rich black shales and positive carbon isotope ($\delta^{13}\text{C}$) excursions, reflecting major disturbances of the global C cycle (Kaiser et al., 2016; Carmichael et al., 2019; Becker et al., 2020). Black shales are sedimentary rocks enriched in organic matter that typically form under oxygen-depleted conditions. This association led to the classical interpretation that black shale deposition is a signature of marine anoxia. However, the link between black shales, $\delta^{13}\text{C}$ excursions, and anoxia is not always straightforward. For example, positive $\delta^{13}\text{C}$ excursions can be recorded in sections where black shales are absent (Da Silva et al., 2020). Conversely, anoxic conditions

do not systematically lead to the deposition of black shales (Carmichael et al., 2019). Moreover, $\delta^{13}\text{C}$ are not the only line of evidence for reconstructing past oxygen-depleted conditions. Other geochemical proxies, such as total C_{org} content, uranium isotopes ($\delta^{238}\text{U}$), and molybdenum isotopes ($\delta^{98}\text{Mo}$), provide additional constraints on the spatial extent, severity, and duration of anoxic episodes (Reershemius and Planavsky, 2021).

Overall, reconstructing environmental conditions from the geological record remains extremely challenging. Because these proxies provide only indirect evidence, the resulting reconstructions are inherently associated with substantial uncertainties. For example, estimates of average atmospheric $[\text{CO}_2]$ across the Devonian compiled by Brugger et al. (2019), based on the dataset of Foster et al. (2017), carry a constant uncertainty of $\sim\pm 1000$ ppm (95 % confidence interval) around an average value of ~ 1500 ppm. Similarly, reconstructions of atmospheric $[\text{O}_2]$ come with uncertainties reaching more than 10 % of the atmospheric composition, depending on the proxy (Mills et al., 2023). These uncertainties are considerable, especially when compared to modern estimates: today, atmospheric $[\text{CO}_2]$ is measured at ~ 430 ppm, and O_2 constitutes 20.95 % of the atmosphere. Furthermore, it is important to distinguish between a globally uniform signal and one that is geographically widespread. Evidence for an event found at multiple sites does not imply that its sedimentary expression was spatially homogenous. In fact, the signature of biological crises in the geological record often varies substantially between regions, reflecting differences in palaeoenvironmental setting and palaeogeography (Carmichael et al., 2019). Consequently, signals recorded at individual sites may capture only part of a larger and more complex environmental perturbation. Specifically, this underscores the importance of integrating multiple datasets and geographical perspectives when reconstructing Devonian OAEs.

1.2.2 Climate models

Numerical climate simulation represents another powerful tool for investigating past environmental conditions. A climate simulation is a numerical representation of Earth's climate system, or parts of it, that captures the physical, chemical, and biological processes governing the atmosphere, oceans, cryosphere, and biosphere. As with geological data, a wide spectrum of climate

simulations exists, ranging from conceptual or box models to fully coupled Earth system models (ESMs).

At one end, conceptual models are based on a few equations and are designed to isolate a limited set of processes to explore the fundamental mechanisms controlling the Earth system. Some include a simplified spatial representation, typically expressed as a small number of interconnected reservoirs (or “boxes”). While these design choices drastically reduce the system dimension and rely on parametrisation to account for a restricted number of processes, they also make these models extremely computationally efficient and therefore highly valuable for exploratory analyses. At the other end, ESMs represent the state-of-the-art approach for simulating the three-dimensional dynamics of the atmosphere and ocean while also including a wide range of biogeochemical processes and interactions between different components of the Earth system. Their high spatial resolution and detailed representation of processes allow them to accurately predict the response of the climate to external perturbations. ESMs are extensively used to investigate future global warming and are by far the most computationally demanding type of climate model (IPCC, 2021).

Between these two extremes lies a third family of models: Earth system models of intermediate complexity (EMICs). These models are designed to investigate transient interactions between climate components, some of which have characteristic response times of several millennia. EMICs typically use a reduced spatial resolution while retaining a large number of climatic components, although each component is generally represented using simpler, more parametrised formulations than in ESMs. Like ESMs, and in contrast to conceptual models, the degrees of freedom in an EMIC exceed the number of adjustable parameters by several orders of magnitude. EMICs bridge the gap between conceptual models and ESMs by combining computational efficiency, reasonable spatial resolution, and the explicit representation of numerous climate system components. As a result, they are particularly well suited for studying climate dynamics on timescales ranging from 10^3 to 10^6 years. In practice, this classification is not rigid, even at the time of its original definition, and the complexity of many models often lies somewhere between these categories (Claussen et al., 2002).

1.2.3 How to reconcile the two?

Geological records and climate models provide complementary approaches for investigating Devonian environmental change. Geological records document the occurrence, timing, and geographical distribution of major perturbations and are therefore essential for identifying potential mechanisms associated with events such as ocean anoxic episodes. However, they rarely allow for the quantification of underlying processes or the identification of the pathways sustaining large-scale anoxia. This limitation is particularly pronounced for the Devonian, as most available records originate from shallow-marine environments. Deep ocean sediments older than ~ 200 Myr have largely been lost to subduction (Scotese and Wright, 2018), resulting in the absence of geological records from the deep ocean. Climate models address these limitations by testing proposed mechanisms within a physically consistent framework. Using boundary conditions informed by geological evidence, they allow different hypotheses to be evaluated and help identify the processes capable of producing the large-scale environmental signals observed in the geological record. Model results can also highlight mechanisms that may not be immediately evident from proxy data alone and thereby suggest new directions for proxy-based research.

Despite this complementarity, direct comparison between models and geological records remains challenging. Proxy data typically provide highly localized information recorded at specific sites, whereas climate models describe the climate system at regional to global scales. Consequently, the two approaches do not describe the past at the same observational scale. Rather than competing descriptions, proxy records and climate models are best understood as complementary perspectives on the same truth (see Fig. 1.6), each resolving features that the other cannot.

1.3 Thesis objectives, method, and outline

1.3.1 Thesis objectives and method

The profound uncertainties surrounding the Devonian may initially appear discouraging, as many aspects of its environmental evolution remain poorly constrained or entirely unknown. Even if such a realization can briefly trigger a scientific existential crisis, it also suggests a considerable exploratory potential of Devonian OAEs research. Definitively explaining the causes of these OAEs will require more than a single thesis. Still, to contribute to this general effort, this thesis investigates several key aspects of these events, primarily through numerical climate simulation and modelling. Specifically, it addresses the following questions:

To what extent did the Devonian continental configuration influence OAEs?

What is the quantitative impact of astronomical forcing on Devonian OAEs? Could it have paced anoxia?

How global was the first-order Kellwasser event, and what magnitude of environmental perturbation would be required to trigger such an OAE?

Addressing these questions requires a climate simulation satisfying several criteria.

- It must include a spatial representation of the ocean to account for regional differences in $[O_2]$ and to distinguish between different marine environments, such as shallow shelves, surface waters, deep ocean, etc.
- It must allow modifications of continental configuration, given that Devonian continental configuration differs markedly from the present and is itself a variable to be explored.
- It needs to accurately represent key processes governing ocean O_2 dynamics, including ocean circulation and the biological pump.

1 | Introduction

- It must be computationally efficient enough to simulate the long timescales associated with Devonian OAEs, which range from 10^4 to 10^6 years (Kabanov et al., 2023), as well as mechanisms operating across similar timescales such as astronomical forcing.

These requirements substantially restrict the range of suitable modelling approaches. Conceptual models generally lack the spatial representation needed to investigate regional $[O_2]$ patterns, whereas fully coupled ESMs are computationally too demanding to simulate the required timescales. Consequently, EMICs represent the most appropriate modelling framework. Among available EMICs, the additional requirement of adjustable continental configurations further narrows the range of viable candidates. Ultimately, the cGENIE model (Ridgwell et al., 2007) was chosen for this thesis, with its main characteristics described in the next subsection.

1.3.2 cGENIE

The carbon-centric Grid-Enabled Integrated Earth system model (cGENIE) is an EMIC (Claussen et al., 2002), designed to simulate long-term interactions between climate, biogeochemical cycles, and ocean–atmosphere processes (Ridgwell et al., 2007).

The physical framework of cGENIE consists of an ocean circulation module (3D), a dynamic–thermodynamic sea ice module (2D), and an atmospheric energy moisture balance module (2D). Together, these components form the C-GOLDSTEIN framework (Edwards and Marsh, 2005; Marsh et al., 2011). The ocean circulation component uses a frictional-geostrophic model based on the reduced physics of the thermocline equations (Edwards et al., 1998). It simulates the transport of heat, salinity, and biogeochemical tracers through advection, convection, and (parametrised) mixing. The atmospheric component is a one-layer model that includes the horizontal transport of heat and humidity in the atmosphere through advection and diffusion by prescribed winds and mixing (Weaver et al., 2001). Precipitation occurs when the relative humidity in this layer exceeds a predefined threshold, and surface albedo and wind stress fields are prescribed. The atmospheric component lacks a dynamic hydrological scheme for continents, setting land evaporation to zero and allocating precipitation to coastal cells based on a runoff map. The sea ice

component consists of a simplified representation of sea ice thermodynamics, following Semtner (1976) and Hibler (1979). Prognostic variables, including ice thickness, areal fraction, and concentration, are used to track the horizontal transport (dynamics) of sea ice and the exchange of heat and freshwater with both the ocean and the atmosphere (Reinhard et al., 2020). Precipitation is instantly routed into the ocean, ignoring the ice, and sublimated water from sea ice is directly added to the atmosphere. A complete description of the model framework, explicitly represented processes, and coupling procedures is provided in Edwards and Marsh (2005) and Marsh et al. (2011).

The biogeochemical framework of cGENIE includes default modules for ocean biogeochemical tracers (BIOGEM, 3D) and atmospheric chemistry (ATCHEM, 2D), while allowing additional optional modules such as sediment geochemistry (SEDGEM, 2D), geochronology of erosion (ROKGEM, 2D), and plankton ecosystem dynamics (ECOGEM, 2D). BIOGEM manages air–sea gas exchange along with the transformations and spatial redistribution of biogeochemical tracers throughout the water column. ATCHEM tracks atmospheric chemical species and computes their partial pressures to represent changes in atmospheric composition. SEDGEM provides a representation of sedimentary stratigraphy and the preservation of biogenic CO_3 and C_{org} deposited on the seafloor (Ridgwell et al., 2007; Hülse and Ridgwell, 2025). ROKGEM is a spatially explicit weathering module that simulates temperature- and runoff-dependent weathering rates, allowing dynamic feedbacks between climate, weathering, and the C cycle over multimillion-year timescales (Colbourn et al., 2013). ECOGEM represents the growth and interaction of an arbitrary number of plankton species, thereby improving the implicit, flux-based parameterisation of the plankton community used in the default model configuration (Ward et al., 2018). Throughout this thesis, specific modules of the biogeochemical framework are enabled or disabled depending on the research question. However, the ECOGEM module is never activated. Consequently, marine biogeochemistry in cGENIE is represented using a nutrient-limited parameterisation of biogenic chemical fluxes (Maier-Reimer, 1993; Ward et al., 2018).

The ocean geometry is typically represented on a 36×36 horizontal equal-area grid with 16 logarithmically spaced levels along the vertical. The equal-area feature of the horizontal grid results from the uniform spacing in the longitude and sine of the latitude. Overall, cGENIE is a coarse-resolution ocean biogeochemistry model that simplifies many physical processes, most notably in its atmosphere. Despite this, the model explicitly resolves numerous climatic

and biogeochemical processes and remains consistent with both data- and model-based estimates (Ridgwell et al., 2007; Marsh et al., 2011; Colbourn et al., 2013; Ward et al., 2018). At the same time, it achieves very high computational efficiency, reaching the order of 10^4 simulated years per day on a single CPU. As such, it is particularly well suited for exploratory studies of long-timescale phenomena such as Devonian OAEs.

1.3.3 Outline

The thesis is organised as three main chapters and one major appendix.

- In **Chapter 2**, we investigate how Devonian continental configuration shaped ocean circulation and $[O_2]$. Using a series of cGENIE sensitivity experiments, we explore interactions between palaeogeography and other key climate components, including atmospheric $[CO_2]$ and $[O_2]$, oceanic dissolved phosphate concentrations ($[PO_4]$), and astronomical forcing. These simulations evaluate the relative impact of these factors on ocean dynamics and $[O_2]$, and clarify how they could precondition the ocean to anoxia. Particular attention is given to how continental configuration influences the sensitivity of ocean $[O_2]$ to other climate variables.
- In **Chapter 3**, we explore the quantitative impact of astronomical forcing on Late Devonian ocean $[O_2]$. To do so, we perform long transient simulations driven by time-varying continental weathering fluxes of PO_4 , reflecting the current leading hypothesis linking astronomical forcing to Devonian OAEs (De Vleeschouwer et al., 2014). In practice, the ROKGEM weathering module is replaced by outputs from a dedicated framework, designed to more accurately capture the sensitivity of precipitation, continental weathering, and nutrient fluxes to astronomical forcing (Sablon et al., 2025). This chapter also examines the spatial heterogeneity of the ocean $[O_2]$ response to astronomical forcing.
- In **Chapter 4**, we focus on the Kellwasser events at the Frasnian-Famennian boundary. Rather than testing a single causal mechanism, we evaluate the magnitude of environmental perturbations required to reproduce the extent of marine anoxia inferred from geological evidence. By combining cGENIE with global and regional proxy constraints, we

aim to establish quantitative benchmarks against which different hypotheses can be assessed. This approach also allows us to examine the potential spatial extent of O₂ depletion during the Lower and Upper Kellwasser events.

- In **Appendix A**, we investigate the ability of cGENIE to accurately reproduce large-scale changes in ocean circulation. Variations in the simulated Atlantic Meridional Overturning Circulation (AMOC) under warming scenarios are compared with CMIP5 model results using the geostrophic approximation, following the approach of Levang and Schmitt (2020). By separating the thermal and haline contributions to the circulation changes, this analysis clarifies how large-scale thermohaline circulation is represented in cGENIE. Although this work is not directly related to Devonian OAEs (hence presented as an appendix), it provides a methodological foundation for the thesis by improving our understanding and confidence in how cGENIE simulates large-scale ocean circulation changes.

We conclude the thesis in Chapter 5 by providing a summary of the main research outcomes and discussing perspectives for future work.

Note: Chapter 2 is based on Gérard et al. (2025), published in *Climate of the Past*. Chapter 3 is based on Gérard et al. (2026), published in *Climate of the Past*. Chapter 4 is based on a paper draft that is currently under preparation for submission. Appendix A is based on Gérard and Crucifix (2024), published in *Earth System Dynamics*. The structure and content of these papers have been adapted to minimise redundancy across chapters.

2

Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

2.1 Introduction

The general objective of the present chapter is to contribute to a better understanding of the intricate interplay of factors preconditioning the ocean to anoxia, which is crucial for unravelling the mechanisms behind Devonian OAEs. A specific challenge for developing plausible anoxic scenarios involving ocean dynamics during the Devonian primarily comes from uncertainties associated with various factors, including atmospheric [CO₂], orbital configuration, and location of continents (Laskar et al., 2011; Foster et al., 2017; Brugger et al., 2019; Marcilly et al., 2022). To meet our general objective, we conduct various sensitivity analyses around those parameters. First, we explore the contribution of Devonian continental configuration and bathymetry to the global

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

mean oceanic O₂ content through modification of ocean circulation patterns (section 2.3.1). Of particular concern are the uncertainties surrounding palaeogeography, especially when it comes to bathymetry, as they exert considerable influence on ocean circulation patterns. The bathymetry of the Devonian is largely unknown because the ocean floor has long since disappeared, as the crust (lithosphere) has been destroyed in subduction zones due to plate tectonics activity (Scotese and Wright, 2018), preventing direct access to deep-ocean data. Therefore, sedimentary data almost exclusively concern the shallow ocean, even though growing evidence points to changes in deeper ocean layers, underscoring the potential influence of deep-ocean dynamics on Devonian OAEs (Chen et al., 2013; Boyer et al., 2014; Turner and Slatt, 2016; Song et al., 2017a; Zhang et al., 2020a; Zhang et al., 2020b). Two distinct approaches exist regarding the representation of bathymetry in Devonian continental reconstructions: one involves a flat bathymetry (Scotese and Wright, 2018), while the other provides a more realistic non-flat bathymetry but with minimal constraints (Vérard, 2019a). The importance of the continental configuration is addressed by comparing results obtained using palaeogeographic reconstructions from Scotese and Wright (2018) with those from Vérard (2019a). Second, we aim to produce an in-depth analysis of ocean dynamics under specific continental configurations (section 2.3.2). We perform sensitivity analyses of three biogeochemical quantities: atmospheric pCO₂ (partial pressure of CO₂), global mean oceanic [PO₄], and atmospheric pO₂ (partial pressure of O₂)¹. We also present a hysteresis experiment to explore how the system reacts in transient conditions. Third, we analyse the effect of astronomical forcing on the large-scale ocean circulation and separate the impact of precession, obliquity, and eccentricity to distinguish their respective contribution to anoxia expansion (section 2.3.3). Together, these three steps allow us to explore the physical contribution of essential components of the Devonian climate system to oceanic oxygenation.

¹Throughout the manuscript, we use partial pressure and concentration interchangeably, as we assume no variations in total atmospheric pressure during the Devonian.

2.2 Methods

2.2.1 Palaeogeographic reconstructions

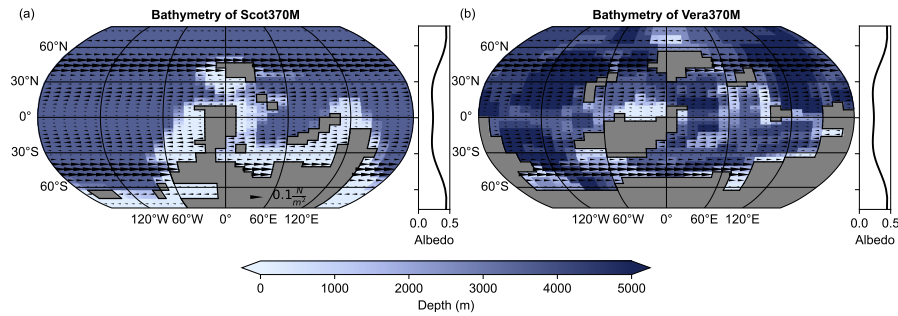


Fig. 2.1 Late Devonian continental configuration. Representation of the Devonian bathymetry (m) at ~ 370 Ma according to (a) Scotese and Wright (2018) and (b) V  rard (2019a) at cGENIE resolution. The meridional albedo profile is shown on the right, and the zonally averaged wind stress profile (function of latitude only) is represented by the black arrows in each panel.

We consider the continental reconstructions produced by Scotese and Wright (2018) and V  rard (2019a). The palaeogeographic reconstructions of Scotese and Wright (2018) span the Devonian from 360 to 420 Ma at ~ 5 Myr intervals, encompassing a total of 13 distinct configurations. They are inferred from a local determination of the palaeoenvironment primarily using lithostratigraphic and palaeontological analyses, with a focus on shoreline regions. Local reconstructions are then extrapolated to address temporal uncertainties and geological gaps, ultimately contributing to a global palaeogeographic reconstruction through interpolation. This process is repeated across multiple sites worldwide to create a detailed understanding of past environmental conditions. The palaeogeographic reconstructions of V  rard (2019a), on the other hand, are obtained through the conversion of a full-plate tectonic model (global coverage with fully closed plate boundaries; see V  rard, 2019b) into a quantified topography (i.e., both orography and bathymetry) following V  rard et al. (2015). With the preliminary version of Panalexis (Panalexis.v0, V  rard, 2019a), these reconstructions are available at 370, 383, 393, 408, and 420 Ma. The approach of Scotese and Wright (2018) has spatial gaps, especially in the ocean, because there is no constraining information. Consequently, the deliverable of Scotese and Wright (2018) features a flat ocean bottom, whereas,

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

by contrast, the geophysical approach of V  rard (2019a) generates global reconstructions, with a detailed representation of deep-ocean bathymetry (V  rard, 2019a). Even if the bathymetry from V  rard (2019a) is poorly constrained, it allows for testing the consequences of such non-flat bathymetry for large-scale ocean dynamics. Sea level references of the two types of reconstructions also differ. Scotese and Wright (2018) align the sea level with the modelled period, whereas V  rard (2019a) consistently uses the present-day volume of ocean water, which, in different sizes of oceanic basins, leads to various sea levels. As we are interested in comparing the two series of reconstructions side by side, we adjusted all V  rard (2019a) reconstructions to conform to the sea level specifications made by Scotese and Wright (2018).

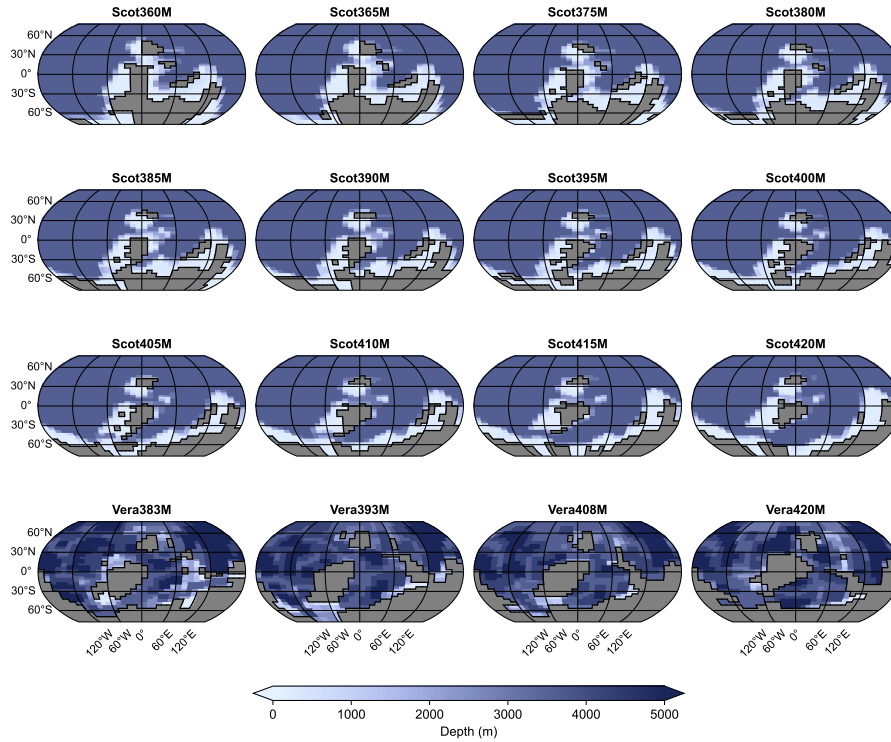


Fig. 2.2 *Ensemble of continental configurations for the entire Devonian Period. Representation of the Devonian bathymetry (m) for 16 continental configurations of the Devonian period. Together with Fig. 2.1, they encompass all 18 reconstructions used in this chapter.*

In our experiments, the ocean geometry is represented on a 36×36 horizontal equal-area grid with 16 logarithmically spaced levels along the vertical (from 80 to 765 m). The experiments use the default cGENIE configuration, as

in Appendix A, including the C-GOLDSTEIN framework and the BIOGEM and ATCHEM modules. We focus here mainly on the contribution of physical mechanisms and, for this reason, consider a scheme of sinking organic matter remineralization independent of temperature. It allows us to better isolate the contribution of physical changes to the biogeochemical variables. A simple zonally averaged wind stress profile is applied to the ocean surface. The albedo profile depends on the latitude only (see Fig. 2.1); there is no explicit dependence on the land–sea mask. Although variations in continental configurations are known, in reality, to affect albedo, our experiments are constrained by the absence of a land surface scheme (i.e., no snow cover, clouds, or ice sheets), limiting the realism, similarly to Cermeño et al. (2022) and Vervoort et al. (2024). Boundary conditions, including a solar constant, were generated using the “muffingen” open-source software suite v0.9.24 (Ridgwell, 2023) and are shown in Fig. 2.1 for different continental configurations. In this chapter, a specific continental configuration is usually referred to as follows: Scot370M (see Fig. 2.1), where the first half indicates the source of the reconstruction (Scotese and Wright, 2018, or Vérard, 2019a) and the second half indicates the age of the configuration (expressed in million years before present). The remaining continental configurations of the Devonian period are shown at cGENIE resolution in Fig. 2.2. All the ocean and atmosphere parameters are based on Cao et al. (2009) and are identical to those from Pohl et al. (2022) (excluding the temperature dependence in the organic matter remineralization scheme).

2.2.2 Description of the experiments

We present three sets of experiments where all simulations were run for 10 000 years until the system reached equilibrium, unless stated otherwise. In the first set, we test continental configurations and solar constants (following Gough, 1981) spanning the whole Devonian. This includes all 13 Devonian continental reconstructions from Scotese and Wright (2018) and 5 from Vérard (2019a), which we test with preindustrial values of atmospheric $p\text{CO}_2$ (280 ppm) and $p\text{O}_2$ (20.95 %) as well as global mean oceanic $[\text{PO}_4]$ ($2.159 \mu\text{mol kg}^{-1}$). Throughout this chapter, these preindustrial values are also referred to as $1 \times p\text{CO}_2$, $1 \times p\text{O}_2$, and $1 \times [\text{PO}_4]$, respectively. Additional simulations with the same solar constant across all 13 Scotese and Wright (2018) continental configurations are then used to remove the impact attributed to variations

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

in the solar constant. The second set explores the combinations of different atmospheric and oceanic chemical concentrations applied to six specific continental reconstructions (three from Scotese and Wright, 2018, and three from V  rard, 2019a). The selected reconstructions are given and justified in section 2.3 corresponding to this experimental set. We used a combination of atmospheric $p\text{CO}_2$, with 1, 2, 4, 8, and $16 \times$ the preindustrial value; global mean oceanic $[\text{PO}_4]$, with 1, 1.25, 1.5, 1.75, and $2 \times$ the modern concentration; and atmospheric $p\text{O}_2$, with 0.4, 0.7, and $1 \times$ the preindustrial value. The third set investigates the astronomical configurations. Values for $p\text{CO}_2$ and $p\text{O}_2$ were selected to capture a substantial portion of the range and uncertainties associated with these parameters throughout the Devonian, with $p\text{CO}_2$ levels from Foster et al. (2017) and Brugger et al. (2019) and $p\text{O}_2$ levels based on Cannell et al. (2022); the range for $[\text{PO}_4]$ was chosen following similar studies on OAEs using cGENIE (Monteiro et al., 2012; H  lse et al., 2021). We have explored the parameter space of the astronomical quantities: eccentricity values of 0, 0.03, and 0.06; obliquity values of 21, 22, 23, 24, and 25° ; and true longitude of the perihelion ranging from 0 to 315° in increments of 45° . Unless explicitly indicated, all the simulations were performed using an eccentricity of 0 (removing any contribution from the precession) and obliquity of 23° . Table 2.1 provides a schematic overview of the three experiment sets.

Set 1	Type	Period (Ma)	$p\text{CO}_2$	$[\text{PO}_4]$	$p\text{O}_2$	Eccentricity	Obliquity	Precession
	Scot	360; 365; 370; 375; 380; 385; 390; 395; 400; 405; 410; 415; 420	1	1	1	0	23°	0°
	Vera	370; 383; 393; 408; 420	1	1	1	0	23°	0°
Set 2	Type	Period (Ma)	$p\text{CO}_2$	$[\text{PO}_4]$	$p\text{O}_2$	Eccentricity	Obliquity	Precession
	Scot	370; 390; 420	1; 2; 4; 8; 16	1; 1.25; 1.5; 1.75; 2	0.4; 0.7; 1	0	23°	0°
	Vera	370; 393; 420	1; 2; 4; 8; 16	1; 1.25; 1.5; 1.75; 2	0.4; 0.7; 1	0	23°	0°
Set 3	Type	Period (Ma)	$p\text{CO}_2$	$[\text{PO}_4]$	$p\text{O}_2$	Eccentricity	Obliquity	Precession
	Scot	370	2	1.25	0.7	0; 0.06	$21^\circ; 25^\circ$	$0^\circ; 90^\circ; 180^\circ; 270^\circ$
	Scot	390	2	1.25	0.7	0; 0.03; 0.06	$21^\circ; 22^\circ; 23^\circ; 24^\circ; 25^\circ$	$0^\circ; 45^\circ; 90^\circ; 135^\circ; 180^\circ; 225^\circ; 270^\circ; 315^\circ$
	Vera	393	2	1.25	0.7	0; 0.06	$21^\circ; 25^\circ$	$0^\circ; 90^\circ; 180^\circ; 270^\circ$

Table 2.1 *Experimental design.* “Type” indicates whether the continental configuration is based on Scotese and Wright (2018) or V  rard (2019a). $p\text{CO}_2$, $[\text{PO}_4]$, and $p\text{O}_2$ are expressed as multiples of preindustrial levels. When variables have multiple values, all possible combinations have been tested.

2.3 Results

2.3.1 Set 1: continental configuration

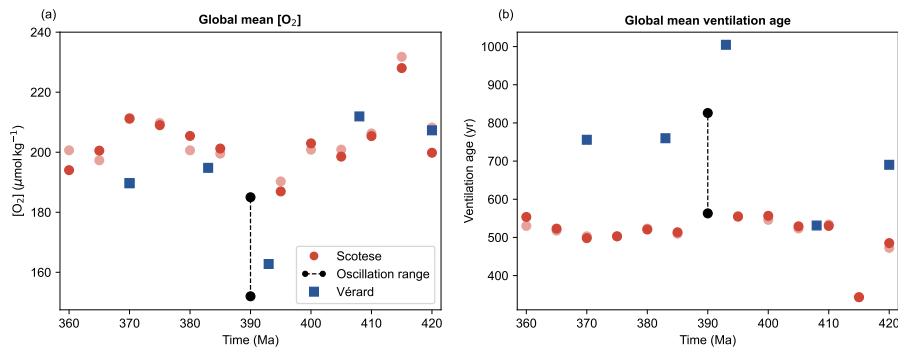


Fig. 2.3 Global average $[O_2]$ and ventilation age for different continental configurations. Mean (a) $[O_2]$ ($\mu\text{mol kg}^{-1}$) and (b) ventilation age (years) of the ocean at equilibrium. Ventilation age is defined as the time since a parcel of water last reached the ocean surface. The red circle and the blue square markers correspond to the simulations conducted using the continental reconstructions of Scotese and Wright (2018) and V  rard (2019a), respectively, with a time-evolving solar constant. The light red colour represents the simulations conducted using the continental reconstructions of Scotese and Wright (2018) with a solar constant of 1322.8 W m^{-2} (computed for 390 Ma). The extreme values of the limit cycle observed in the continental configuration of Scot390M are highlighted in black in both panels, representing the amplitude of the oscillations.

The impact of palaeogeographical evolution on oceanic oxygenation and ventilation using the continental reconstructions of Scotese and Wright (2018) (red dots) and V  rard (2019a) (blue squares) is shown in Fig. 2.3. The two sets of reconstructions generate fairly similar mean $[O_2]$ but with substantial differences in ventilation ages. Ventilation age is defined as the time since a parcel of water last reached the ocean surface. Simulations using reconstructions of V  rard (2019a) generally present higher ventilation ages because the ocean floor is deeper, increasing the time needed by water masses to reach these depths. In our experimental design, seafloor depth emerges as the primary factor influencing average ventilation age, as no substantial differences were observed in the number or extent of deep water formation regions between the Scotese and Wright (2018) and V  rard (2019a) reconstructions. Additionally, when the ocean floor depth was artificially reduced in the V  rard (2019a) reconstructions, to align with that of Scotese and Wright (2018), the average

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

ventilation age decreased, reaching similar values to those observed with the Scotese and Wright (2018) reconstructions. Figure 2.3a and b show that the global average $[O_2]$ and ventilation age evolve in opposite directions ($r^2 = 0.91$ with p-value = 4.3×10^{-7} and $r^2 = 0.93$ with p-value = 0.008 for the set of reconstructions from Scotese and Wright (2018) and V  rard (2019a), respectively). This suggests that the variations in $[O_2]$ are primarily explained by changes in ventilation, caused by modifications in ocean circulation dynamics induced by the prescribed differences in continental configuration. Second-order variations in $[O_2]$ observed in our simulations can be attributed to changes in O_2 solubility and modifications in exported organic matter (biological pump), which are influenced by alterations in the solar constant and differences in continental configuration. All the simulations converge towards a stable steady state, except Scot390M. The latter is characterized by stable self-sustained oscillations with a period of ~ 3000 years, portrayed by the dashed black line in Fig. 2.3a and b. Continental changes induce non-monotonic variations in $[O_2]$ through time, with some of them reaching 30 and $50 \mu\text{mol kg}^{-1}$ between consecutive equilibrium states using the reconstructions of Scotese and Wright (2018) and V  rard (2019a), respectively. Considering the global scale of these variations, they reflect considerable modifications in the amount of dissolved O_2 in the ocean. Notably, the variations in O_2 intensify with depth and culminate in maximal values within the deepest layers of the ocean. At these depths, the oscillation in Scot390M can reach an amplitude of more than $100 \mu\text{mol kg}^{-1}$.

Millennial oscillations in the ocean circulation have been reported in several oceanic models (Sakai and Peltier, 1997; Thornalley et al., 2009; Peltier and Vettoretti, 2014; S  vellec and Fedorov, 2014; Li and Yang, 2022; Vettoretti et al., 2022). They generally arise from an interplay between advective and convective feedbacks. Given our experimental design, the emergence of these oscillations could be attributed to either the specific choice of continental configuration or the solar constant. To verify the role of the former, additional simulations with the Scotese and Wright (2018) reconstructions were conducted using the same solar constant (the one from Scot390M). The equilibrium state of these simulations is represented by the light red circles in Fig. 2.3a. Variations in $[O_2]$ are small, on average lower than $3 \mu\text{mol kg}^{-1}$, compared with the corresponding simulations with varying solar constants, suggesting that the solar constant only has a second-order impact on global mean oceanic $[O_2]$. This also demonstrates that changes in continental configurations can, alone,

induce variations in the nature of the solution of the system (apparition of an oscillation). Similar millennial oscillations in the ocean circulation have been reported by Pohl et al. (2022) under early Paleozoic continental configurations. Here, we demonstrate that such oscillations can also develop with a Devonian continental configuration.

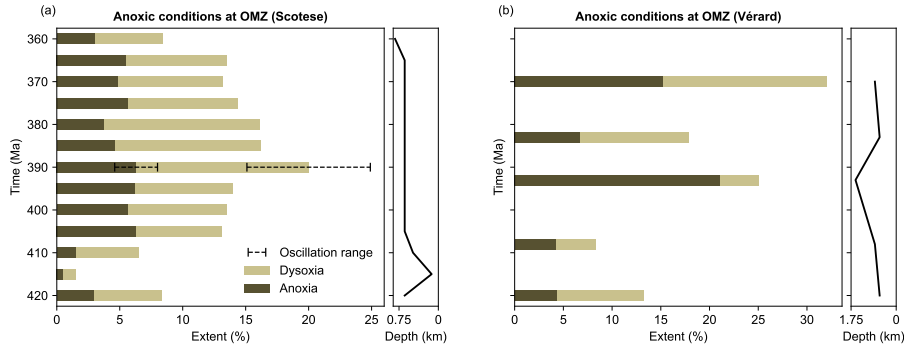


Fig. 2.4 OMZ extent variations with continental configuration. Anoxic ($[O_2] < 6.5 \mu\text{mol kg}^{-1}$) and hypoxic ($[O_2] < 62.5 \mu\text{mol kg}^{-1}$) extent at the OMZ (expressed as a percentage of the horizontal layer) for the simulations conducted using the continental reconstructions of (a) Scotese and Wright (2018) and (b) V  rard (2019a). Here, the OMZ is defined as the horizontal layer of the ocean that has the greatest anoxic extent, and its depth is given by the black line on the right of each panel. The dashed black line represents the amplitude of the oscillation observed in Scot390M.

The extent of the oxygen minimum zone (OMZ) of all the continental reconstructions is shown in Fig. 2.4a and b. Here, the OMZ refers to the horizontal layer of the ocean that has the greatest anoxic extent. The anoxic or dysoxic extents are defined as the percentage of grid cells, within a horizontal layer, with $[O_2]$ under 6.5 and $62.5 \mu\text{mol kg}^{-1}$, respectively (after Sarr et al., 2022). Variations in anoxic extent across simulations with different continental reconstruction types (Scotese and Wright, 2018, vs. V  rard, 2019a) are generally substantial: choosing one type of reconstruction over another has a sizeable impact on the simulated OMZ. The reconstructions of Scotese and Wright (2018) tend to produce a shallower and much smaller OMZ, while those of V  rard (2019a) produce a very widespread anoxic extent, with the OMZ sometimes being very deep and reaching 20 % of the horizontal layer. The increased anoxic levels from the V  rard (2019a) configurations are attributed to a deeper ocean that increases the average age of water masses and a non-flat bathymetry that introduces more complex circulation patterns, generating additional regions with older water masses. Also, the lack of shallow shelves in the V  rard

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

(2019a) reconstructions reduces upper-ocean deoxygenation and shifts anoxia to the deeper ocean. Nevertheless, a common pattern emerges. For both reconstruction types, the Middle (~ 393 – 382 Ma) and Late (~ 382 – 359 Ma) Devonian exhibit higher susceptibility to reaching an OAE due to the broader average OMZ extent associated with these periods, and this is consistent with the temporal distribution of observed OAEs (see Fig. 22.13 in Becker et al., 2020).

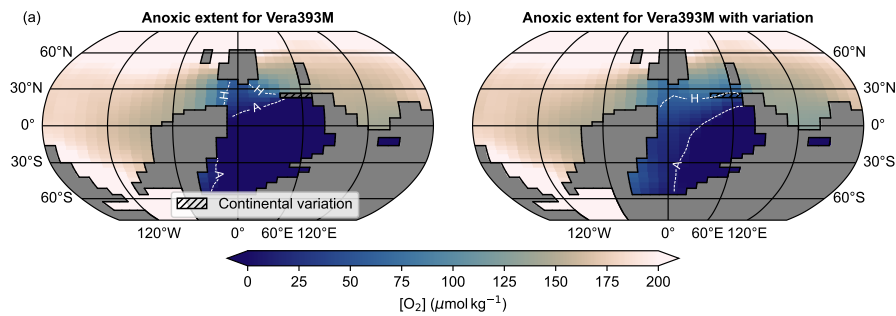


Fig. 2.5 *Impact of a small variation in the continental configuration on ocean anoxia.* The oceanic $[O_2]$ ($\mu\text{mol kg}^{-1}$) is shown at 1.5 km depth. Panels (a) and (b) represent the original and modified Vera393M configuration, respectively. The A and H lines respectively outline the boundaries of the anoxic and hypoxic regions, with thresholds set at 6.5 and $62.5 \mu\text{mol kg}^{-1}$ (after Sarr et al., 2022). The continental configuration in (a) is valid at 1.5 km depth. Grid cells representing land at this depth are shaded grey. Hence, it differs slightly from that in Fig. 2.2, which represents surface bathymetry.

Now we focus on the impact of a specific small change in the continental configuration on the extent of anoxia. We created a variation of the Vera393M continental configuration, represented in Fig. 2.5b. The only modification is the removal of the three continental grid points represented by hatching in Fig. 2.5a. It was designed to alter an important seaway, following a common practice in climate modelling (Lawver and Gahagan, 2003; Von Der Heydt and Dijkstra, 2006; Yang et al., 2014). Comparison of Fig. 2.5a and b shows that the alternative configuration has a smaller OMZ and is, overall, substantially more oxygenated than the original one. The anoxic extent is reduced by 10 % (from 21 % to 11 %) at the OMZ, here at 1.5 km, but the reduction can increase up to 17 % at 2.5 km depth, withdrawing the entire anoxic region. The increase in O_2 content is associated with a negative water age anomaly. Overall, waters are younger and more oxygenated across the entire interior basin, owing to the advection of young water masses that were previously blocked by continental

grid cells. These simulations are evidence that minor continental changes, in the Devonian, may have a large impact on ocean dynamics and $[O_2]$.

2.3.2 Set 2: geochemical state and climate forcing

Contribution of PO_4 and pO_2

Having established the contribution of the continental configuration to variations in oceanic oxygenation during the Devonian, our next experimental set (Set 2) involves the investigation of the system dynamics under the modification of three prescribed quantities: atmospheric pCO_2 , global mean oceanic $[PO_4]$, and atmospheric pO_2 . Here, atmospheric pCO_2 is used as a climate forcing, where a doubling of pCO_2 induces an increase of 4 W m^{-2} in the radiative forcing, which corresponds to a warming of $\sim 3^\circ \text{C}$ in our simulations. For each variable, we test between three and five different values, as explained in section 2.2.2, but implementing these modifications across all 18 continental configurations would result in a large number of runs and data. Therefore, we only selected three reconstructions from Scotese and Wright (2018) and V  rard (2019a) to perform the investigation: one for the Early, Middle, and Late Devonian. We selected periods for which both types of reconstructions are available, as we also aim to compare them side by side. Two natural choices are the continental configurations of 370 and 420 Ma, as they are the only two periods matching perfectly across both reconstruction sets. We added the Scot390M configuration due to its oscillatory behaviour, which leads us to choose Vera393M as it corresponds to the closest reconstruction from V  rard (2019a).

The impact of global mean oceanic $[PO_4]$ and atmospheric pO_2 on benthic ocean anoxia is shown in Fig. 2.6 for all the chosen continental configurations (the colours refer to different Devonian periods). The benthic ocean is defined as seafloor grid cells deeper than 2 km below sea level. Throughout our investigations, examining the benthic ocean has proven to be sufficient as every change in dynamics that affects the global ocean was systematically captured by the benthic ocean. In our experimental setup, the contribution of $[PO_4]$ and atmospheric pO_2 to ocean $[O_2]$ is straightforward and systematic (see Fig. 2.6). An increase in $[PO_4]$ leads to a greater extent of oceanic anoxia because of an increase in primary productivity and the related remineralization

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

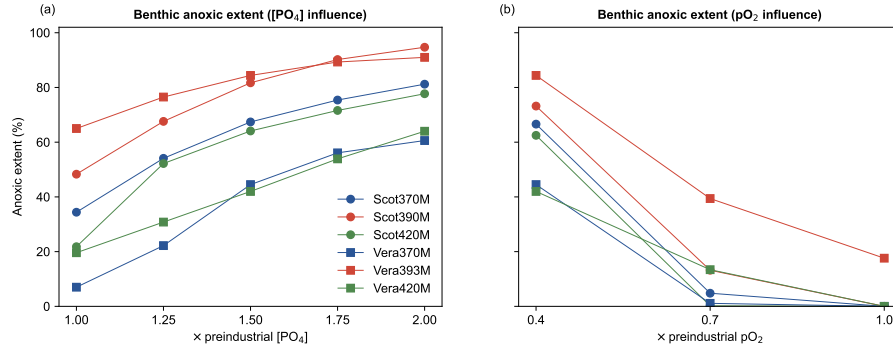


Fig. 2.6 Influence of [PO₄] and pO₂ on benthic anoxia. Evolution of the benthic anoxic extent (expressed as a percentage of the seafloor) as a function of (a) global mean oceanic [PO₄] and (b) atmospheric pO₂ for different continental reconstructions of the Early, Middle, and Late Devonian. Benthic anoxia is computed here as the percentage of the seafloor deeper than 2000 m characterized by $[O_2] < 6.5 \mu\text{mol kg}^{-1}$. Simulations were performed using $4 \times p\text{CO}_2$ and $0.4 \times p\text{O}_2$ in (a) and using $4 \times p\text{CO}_2$ and $1.5 \times [\text{PO}_4]$ in (b). This $p\text{CO}_2$ was chosen to avoid interference from limit cycles, which only occur at 1 and $2 \times p\text{O}_2$.

through microbial processes. The atmospheric pO₂ decrease has a substantial yet obvious effect, where less O₂ correlates with a greater anoxic extent. Here, the continental configuration modulates the impact of [PO₄] and pO₂ on benthic ocean anoxia, but it does not alter their overall dependency. The percentage of the benthic ocean that has reached the anoxic state is shown in Fig. 2.7 as a function of atmospheric pCO₂. The role of atmospheric pCO₂ in benthic anoxia is less straightforward than that of pO₂ and [PO₄], as continental configuration greatly conditions the amplitude and even the sign of the effect of a pCO₂ increase. For instance, Scot370M and Vera370M (blue curves in Fig. 2.7a and b) reveal opposite trends of the anoxic extent with rising pCO₂. Furthermore, for Scot390M, in red in Fig. 2.7a, we obtain non-monotonic dependencies of anoxia on pCO₂. We further analyse these aspects in the next subsections.

Contribution of pCO₂

For every continental configuration used in Set 2, the rise in pCO₂ induces two processes with opposite effects on [O₂]. First, the decrease in O₂ solubility at the surface following a temperature elevation leads to negative [O₂] anomalies, which then propagate throughout the benthic ocean by the deep circulation.

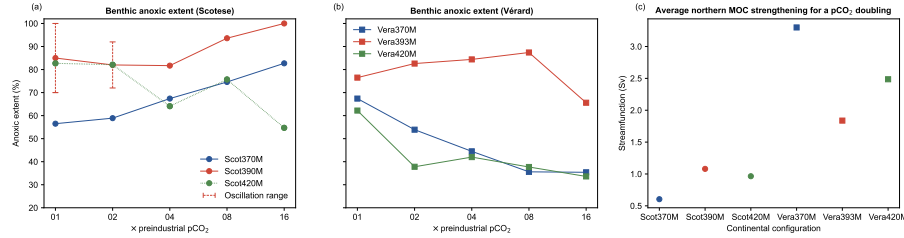


Fig. 2.7 Influence of $p\text{CO}_2$ on benthic anoxia and ocean circulation. Evolution of the benthic anoxic extent (expressed as a percentage of the seafloor) as a function of $p\text{CO}_2$ for Early, Middle, and Late Devonian simulations conducted using the continental reconstructions of (a) Scotese and Wright (2018) and (b) V  rard (2019a). The green line in panel (a) is dotted to indicate multistability, meaning that this curve is one of many possible trajectories for the evolution of benthic anoxia under varying $p\text{CO}_2$; this specific trajectory fits the experimental design of this set. The dashed red lines in panel (a) represent the range of the stable oscillations. In the presence of a limit cycle, the red square denotes the intermediate value between the extrema of the oscillations. Every simulation was performed using $1.5 \times [\text{PO}_4]$ and $0.4 \times p\text{O}_2$. (c) Average northern meridional overturning circulation (MOC) strengthening ($1 \text{ Sv} \equiv 10^6 \text{ m}^3 \text{ s}^{-1}$) following a $p\text{CO}_2$ doubling using the continental reconstructions of (a) and (b).

Second, the northern MOC is systematically strengthened with each doubling of $p\text{CO}_2$, improving the ventilation and reducing the extent of benthic anoxia. We interpret this strengthening as the result of a seesaw effect between the southern and northern water masses, whereby the weakening of the southern convection cell allows for a deeper propagation of the northern cell (see Fig. 2.8a and b). Although not straightforward because of the zonal average of ocean circulation, analysis of $[\text{O}_2]$ patterns confirms that deep-water formation of the northern cell consistently occurs at high northern latitudes across reconstructions. However, the magnitude of the seesaw phenomenon varies greatly from one reconstruction to another, leading to differences in results emerging from varying relative contributions of temperature vs. circulation to oceanic $[\text{O}_2]$ changes. Specifically, Scot370M (blue curve in Fig. 2.7a) is the result of a scenario where enhanced ventilation is unable to compensate for the surface O_2 solubility loss, resulting in a net increase in the benthic anoxic extent with $p\text{CO}_2$ (see Fig. 2.8c). Conversely, Vera370M (blue curve in Fig. 2.7b) is a case where the strengthening of the MOC exceeds the solubility loss, increasing benthic $[\text{O}_2]$ in response to global climate warming. Throughout our testing, we found that configurations of Scotese and Wright (2018) typically align with the first category, whereas the ones from V  rard (2019a) belong to the second. For the reconstructions of Scotese and Wright (2018), the

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

alterations of the overturning cell are small, reaching an average strengthening of 1 Sv across the entire ocean, while it often reaches 2 to 3 Sv with those from V  rard (2019a) (see Fig. 2.7c).

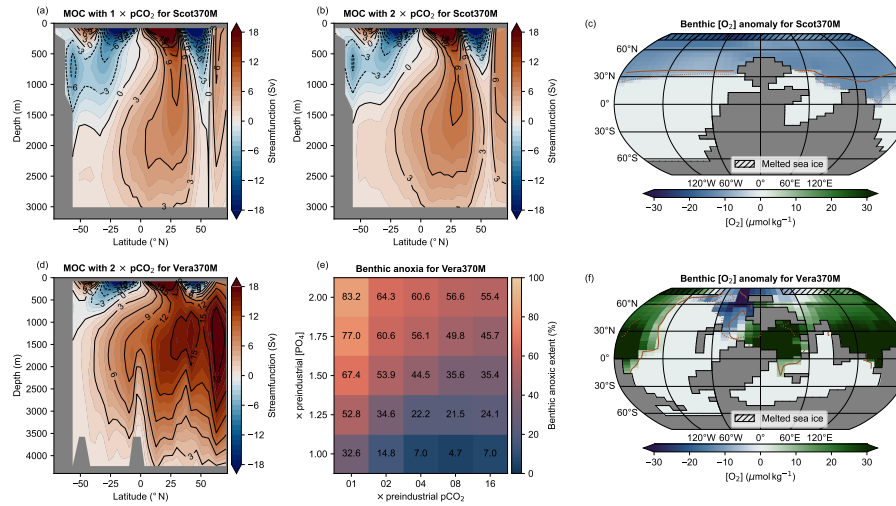


Fig. 2.8 Oceanic circulation and oxygenation for the 370 Ma simulations. (a, b) MOC for the 370 Ma simulation using the reconstruction of Scotese and Wright (2018) at (a) $1 \times p\text{CO}_2$ and (b) $2 \times p\text{CO}_2$. (c) Benthic $[\text{O}_2]$ anomaly between 4 and $2 \times p\text{CO}_2$ for Scot370M. The dotted and solid dark orange curves represent the extent of the benthic anoxic region with 2 and $4 \times p\text{CO}_2$, respectively. (d) Same as (b) but for Vera370M. (e) Percentage of the benthic ocean that reached the anoxic state as a function of $p\text{CO}_2$ and $[\text{PO}_4]$ for Vera370M. The row with $1.5 \times [\text{PO}_4]$ is identical to the blue curve in Fig. 2.7b. (f) Benthic $[\text{O}_2]$ anomaly between 1 and $2 \times p\text{CO}_2$ for Vera370M. The dotted and solid dark orange curves represent the extent of the benthic anoxic region with 2 and $1 \times p\text{CO}_2$, respectively. Except in (e), all the simulations presented here have been performed using $1.5 \times [\text{PO}_4]$ and $0.4 \times p\text{O}_2$.

In some cases, effects related to nutrient availability may determine the total effect on $[\text{O}_2]$. For example, in Vera370M, anoxia generally decreases when $p\text{CO}_2$ increases because of the increase in circulation. In some simulations, though, we see the opposite (see Fig. 2.8e). This occurs at relatively low $[\text{PO}_4]$ and when the ocean is already well-oxygenated. As $[\text{PO}_4]$ decreases, the benthic anoxic boundary shifts southward (see Fig. 2.8c) and may reach areas less affected by MOC strengthening. In these simulations, even though circulation strengthens in response to rising temperatures, the active circulation cell does not efficiently ventilate the anoxic areas left in the benthic ocean. Consequently, the main cause of $[\text{O}_2]$ change is solubility loss, leading to a subsequent decrease in $[\text{O}_2]$. The same reasoning can be applied to explain

the small mismatch between Vera370M and Vera420M (blue and green curves in Fig. 2.7b) when increasing from 2 to $4 \times \text{pCO}_2$.

Another mechanism contributing to ocean oxygenation is associated with the absence of sea ice due to its melting that occurs when increasing from 1 to $2 \times \text{pCO}_2$ (see Fig. 2.8f). This melting leads to large increases in the number of convection sites and vertical mixing, globally improving the ventilation of the benthic ocean. Although this contribution is almost absent from Fig. 2.7, it can be seen in Fig. 2.8e where the major oxygenation occurs when increasing from 1 to $2 \times \text{pCO}_2$. Given the strong MOC simulated in Vera370M (see Fig. 2.8d), the positive O_2 anomaly easily spreads throughout the majority of the benthic ocean, leading to the observed substantial reduction in anoxia extent. The effect of sea ice melting is also present for Scot370M but generally does not appear when increasing from 1 to $2 \times \text{pCO}_2$. This is because the overturning cell of Scot370M is much weaker than the one from Vera370M (see Fig. 2.8b and d), which prevents the positive O_2 anomalies from reaching the anoxic water masses, mainly located in the southern part of the ocean (see Fig. 2.8c). While the influence of sea ice melting on the extent of benthic anoxia is not always striking, it consistently impacts the average benthic $[\text{O}_2]$, highlighting its substantial oxygenating effect. Together, all these mechanisms encompass the relevant processes to understand how large-scale ocean dynamics affect benthic anoxia for Scot370M, Vera370M and Vera420M.

State transitions in global ocean circulation

We now analyse the remaining curves in Fig. 2.7 in depth, along with their associated ocean characteristics. As previously mentioned, the anoxic extent in Scot390M (red curve in Fig. 2.7a) decreases with pCO_2 from 1 to $4 \times \text{pCO}_2$ and then increases until $16 \times$. We find that the limit cycle identified for this continental configuration (see section 2.3.1) occurs at 1 and $2 \times \text{pCO}_2$. For these concentrations, the system has self-sustained oscillations with a period of 3000 years featuring variations in their amplitude (see Fig. 2.9a and b). These oscillations, with some amplitudes reaching up to $100 \mu\text{mol kg}^{-1}$, move the benthic ocean back and forth from oxic to globally anoxic conditions. Nevertheless, the limit cycle shifts the system towards more anoxic conditions on average. Hence, the decrease in oscillation amplitude leads to the reduction of the benthic anoxic extent, explaining the trend observed for Scot390M in Fig. 2.7a between 1 and $4 \times \text{pCO}_2$. Upon reaching $4 \times$ the preindustrial levels, we

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

find the same behaviour as in Scot370M, wherein an increase in $p\text{CO}_2$ induces a reduction of available O_2 at the benthic level through the loss of solubility.

The configuration Scot420M (green curve in Fig. 2.7a) is most puzzling, with the anoxic extent decreasing, increasing, and decreasing again as $p\text{CO}_2$ levels rise. Yet, upon inspection, the circulation does not undergo large-scale changes that could explain this behaviour. Additional simulations, involving different initial conditions, have revealed that with the Scot420M configuration, the system exhibits pronounced multistability: the system appears to almost randomly converge towards a distribution of potential states. Which state the system reaches depends on both the initial $p\text{CO}_2$ condition and the rate at which we converge toward a specific $p\text{CO}_2$, without clear rules. The range of accessible states also depends on the imposed $p\text{CO}_2$. Specifically, we found that the anoxic extent obtained with $8 \times p\text{CO}_2$ could vary up to more than 20 % against less than 10 % with $16 \times p\text{CO}_2$. Within the spectrum of states that the system can reach, a limit cycle exists, different from the one in Scot390M (see Fig. 2.9a and b). The identified oscillation has a period of ~ 5000 years and can only be accessed under $2 \times p\text{CO}_2$ (see Appendix B for a more detailed explanation). Due to this multistability, Scot420M (green curve in Fig. 2.7a) only depicts one of the many potential trajectories of benthic anoxia across varying $p\text{CO}_2$ levels (therefore represented as dotted). As a consequence, investigating physical mechanisms with this continental configuration and forcings is particularly challenging.

Vera393M (red curve in Fig. 2.7b) also shows a non-monotonic behaviour. Between 1 and $8 \times p\text{CO}_2$, the warming is linked to an increase in the benthic anoxic extent, whereas going from 8 to $16 \times p\text{CO}_2$ results in a reduction of benthic anoxia. Vera393M stands out among the six continental configurations examined in this section: it is the only one that generates a scenario where water masses of southern origin dominate the deep ocean (see Fig. 2.9d). In other configurations, continental cells in the southernmost latitudinal band prevent the formation of deep water there. The southern circulation relies on a reduced number of convection sites due to the position of the continents. As a result, the ocean exhibits, on average, lower oxygenation levels compared to reconstructions with a dominant northern overturning cell. As $p\text{CO}_2$ increases, the northern circulation cell intensifies, gradually taking over the southern cell because of the seesaw effect (see Fig. 2.9d–f). Although the northern overturning cell strengthens with each increase in $p\text{CO}_2$, full penetration of related deep waters into the benthic ocean is partially prevented by the

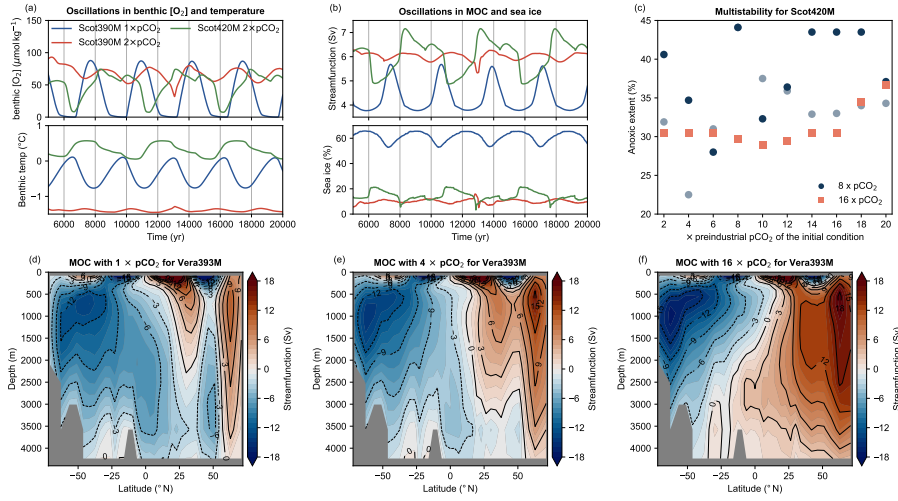


Fig. 2.9 Nonlinear responses of ocean circulation, oxygenation, and climate to $p\text{CO}_2$ and continental configuration. Representation of the limit cycles in (a) benthic $[\text{O}_2]$ ($\mu\text{mol kg}^{-1}$), benthic temperature ($^{\circ}\text{C}$), (b) maximum MOC strength (Sv), and northern sea ice extent (%) for different continental configurations and atmospheric $p\text{CO}_2$. The northern sea ice extent is defined here as the average sea ice cover beyond 60°N . These simulations were run for 20 000 years using 1.25 and $1.75 \times [\text{PO}_4]$ for Scot390M and Scot420M, respectively, and $0.7 \times p\text{O}_2$. These $p\text{O}_2$ and $[\text{PO}_4]$ values were selected to illustrate the full extent of the influence of the limit cycles on the system. (c) Multistability associated with $8 \times p\text{CO}_2$ (blue) and $16 \times p\text{CO}_2$ (red) considering 10 different initial conditions for Scot420M using $1 \times [\text{PO}_4]$ and $0.4 \times p\text{O}_2$. For these simulations, the change from initial to final $p\text{CO}_2$ occurs instantaneously (i.e., in one model iteration), except for the simulations represented by light blue dots, where the change occurs gradually over 5000 years. Measure of the MOC strength in Sverdrups (Sv) as a function of latitude and depth under (d) $1 \times p\text{CO}_2$, (e) $4 \times p\text{CO}_2$, and (f) $16 \times p\text{CO}_2$ for Vera393M. These simulations were performed using $1.5 \times [\text{PO}_4]$ and $0.4 \times p\text{O}_2$.

southern cell. The main contributions affecting the benthic $[\text{O}_2]$ are the slowdown of the southern cell and the decrease in solubility of surface waters, both contributing to the expansion of the anoxic extent. Only upon going from 8 to $16 \times p\text{CO}_2$ do deep waters of northern origin efficiently propagate into the benthic ocean, leading to increased $[\text{O}_2]$ and the reduction of benthic anoxic extent.

Long time response – hysteresis

The presence of multiple equilibria and state transitions in the global ocean circulation has motivated us to conduct a hysteresis simulation to identify pos-

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

sible transient behaviours, potential signs of bistability, and their implications for the ocean time response. Bistability arises when a system, subject to the same external conditions, can settle into one of two distinct stable equilibria depending on its initial conditions. The hysteresis simulation is performed with the Scot390M continental configuration over 150 000 years and involves a linear increase and decrease in $p\text{CO}_2$ between 1 and $16 \times$ the preindustrial levels, as shown in Fig. 2.10a. Figure 2.10b shows the transient benthic $[\text{O}_2]$ evolution for increasing (blue) and decreasing (red) $p\text{CO}_2$.

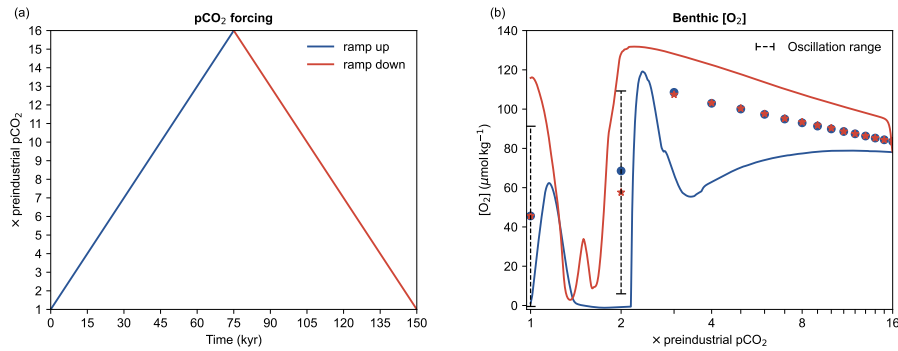


Fig. 2.10 Results of a hysteresis experiment. (a) Schematic of atmospheric $p\text{CO}_2$ forcing for the hysteresis experiment. The blue and red lines show the transient increase and decrease in the forcing, respectively. (b) Hysteresis curves of average benthic $[\text{O}_2]$ ($\mu\text{mol kg}^{-1}$) as a function of $p\text{CO}_2$ for Scot390M with $1.25 \times [\text{PO}_4]$ and $0.7 \times p\text{O}_2$. The x axis is logarithmic. The blue and red curves represent the transient evolution of the average benthic $[\text{O}_2]$ when the $p\text{CO}_2$ forcing increases and decreases, respectively. The blue dots and red stars are the stable equilibrium of the system. The dashed black lines represent the amplitude of the oscillations observed for these stable equilibria. Under $2 \times p\text{CO}_2$, the oscillation manifests only for the red star and not the blue dot.

Given that the simulation restarts from a stable state (previous spin-up of 10 000 years) and considering the slow evolution of the forcing ($0.056 \text{ ppm yr}^{-1}$), the system can be assumed to be almost in equilibrium. We further show the stable steady state of the system for specific $p\text{CO}_2$ values with dots and stars in Fig. 2.10b, starting from the blue and red curves, respectively. When the system reaches stable oscillations, the dots and stars are placed at the intermediate value between the extremes of the limit cycle. Comparison of these markers reveals no clear signs of bistability, yet discrepancies arise for $2 \times p\text{CO}_2$, where the blue and red markers do not coincide. Under $2 \times p\text{CO}_2$, the system converges towards stable oscillations when starting from warm conditions and to a stable steady state when starting from cold conditions.

For the Scot390M configuration, oscillations manifest themselves for specific $p\text{CO}_2$ values within an interval surrounding $2 \times p\text{CO}_2$. Additional simulations have located the lower and upper boundaries of this interval around 1.8 and $2.2 \times p\text{CO}_2$, respectively. Our findings indicate that to trigger these oscillations, atmospheric $p\text{CO}_2$ must fall within this range but that the system also needs to come from warmer conditions (i.e., higher $p\text{CO}_2$). Hence, we qualify the lower boundary of this oscillation interval as “asymmetrical”, indicating that it only acts as a boundary when the limit cycle is already present. This feature of the oscillation interval accounts for the emergence of two distinct stationary regimes reached under $2 \times p\text{CO}_2$, as shown in Fig. 2.10b. In addition, benthic $[\text{O}_2]$ displays substantial hysteresis, indicating a very slow ocean time response when the CO_2 varies.

2.3.3 Set 3: astronomical forcing

The final set of experiments (Set 3) explores the astronomical forcing contribution to variations in $[\text{O}_2]$ through changes in large-scale ocean dynamics. Given the wide range of considered astronomical configurations (see section 2.2.2), we limited our analysis to the Scot370M, Scot390M, and Vera393M continental configurations. These reconstructions were chosen as they encompass all the relevant dynamics identified in the previous section, namely sea ice melting, the presence of two overturning cells, and oscillations.

Figure 2.11 shows how the dysoxic extent of the benthic ocean varies across a range of extreme astronomical configurations for Scot370M and Vera393M. These reconstructions were selected arbitrarily to compare the astronomical signal between substantially different continental configurations. The fixed atmospheric $p\text{O}_2$ is high enough to almost entirely remove the benthic anoxic extent, leaving meaningful variations only in the dysoxic extent. For Scot370M, the results indicate that obliquity has the largest effect on the benthic dysoxic extent, increasing it up to 13 % (see LOLE and HOLE in Fig. 2.11a). The predominance of the obliquity is not so surprising because obliquity has, among the astronomical parameters, the greatest impact on temperature at high latitudes, where deep-oceanic convection takes place. In comparison, eccentricity and precession play a relatively minor role, resulting in maximal variations of around 2 % of the dysoxic extent in Fig. 2.11a; for intermediate values of obliquity (not shown here), this impact can increase to 5 %. For

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

Vera393M, the astronomical forcing has a smaller, yet still substantial, impact on the benthic dysoxic extent of poorly oxygenated benthic waters, about half the amplitude identified for Scot370M. Across all astronomical configurations considered, the maximal difference in the benthic dysoxic extent is 15.6 % for Scot370M against 8.5 % for Vera393M. Still, the response remains dominated by obliquity, with a lesser contribution from eccentricity and precession. These results also highlight that the continental configuration can modulate the influence of the astronomical forcing on the system. This modulating aspect was already introduced in Sarr et al. (2022) for the Late Cretaceous, where some astronomical configurations could induce up to 50 % of the water volume to become anoxic in enclosed and already poorly oxygenated basins (central Atlantic) compared to 0 % in more open basins (south of the Walvis Ridge).

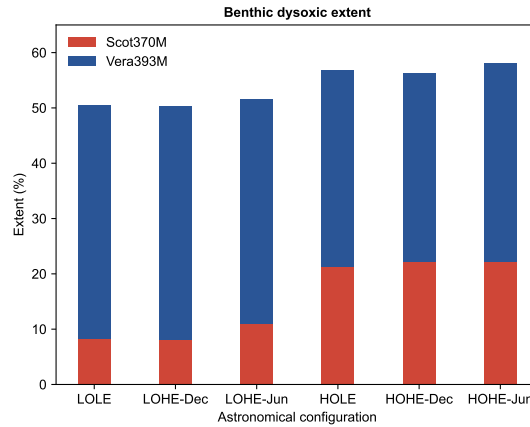


Fig. 2.11 Astronomical forcing influence on benthic dysoxic extent. Percentage of the benthic ocean that reached dysoxia under different astronomical configurations for Scot370M (red) and Vera393M (blue). Benthic dysoxia is computed here as the percentage of the seafloor deeper than 2000 m characterized by $[O_2] < 62.5 \mu\text{mol kg}^{-1}$. LO (low obliquity) and HO (high obliquity) correspond to simulations where obliquity is set to 21° and 25° , respectively. LE (low eccentricity) and HE (high eccentricity) correspond to simulations where eccentricity is fixed at zero to remove any contribution from precession and 0.06, respectively. In HE simulations, precession effects are maximized, with the different months indicating when in the year the perihelion is reached. All simulations were performed using $2 \times p\text{CO}_2$, $1.25 \times [\text{PO}_4]$, and $0.7 \times p\text{O}_2$.

Figure 2.12 shows the influence of the astronomical forcing on the nature of the solution for Scot390M expressed as eccentricity–precession maps for each obliquity value considered. Each dot represents a simulation at equilibrium for a certain astronomical configuration, with the colour representing the type of equilibrium reached by the system: red for a stable steady state and blue for

stable oscillations. Results in Fig. 2.12 demonstrate that each astronomical parameter can shift the equilibrium type of the system, transitioning from stable oscillations to a stable steady state or vice versa. Obliquity and eccentricity are the main factors determining the equilibrium type, with precession being secondary. The importance of obliquity and eccentricity is well-explained by their influence on annual mean temperature beyond 60° N. Figure 2.12 also shows the range of astronomical configurations for which stable oscillations occur. At low obliquity and low eccentricity, the high latitudes become too cold to support stable oscillations, providing a cold boundary for the oscillation. At higher obliquity, stable oscillations also tend to disappear, although the threshold depends on the precise value of eccentricity, with precession becoming critical only when obliquity is at 23°. For these configurations, the high latitudes become too warm, indicating a warm boundary for the oscillation. Additional simulations have shown that the oscillation interval also features the asymmetrical nature identified in the hysteresis section: oscillations emerge only when the system is started from initial conditions beyond the warm boundary.

2.4 Discussion

2.4.1 Implications for current hypotheses about Devonian OAEs

We used cGENIE to investigate the contribution of continental configuration, geochemical states, and astronomical forcing to Devonian anoxia. First, we found that the continental configuration plays a central role throughout our study, not only through its direct impact on ocean dynamics and [O₂], but also through modulating the influences of pCO₂, oceanic [PO₄], pO₂, and astronomical forcings. The differences between reconstructions from Scotese and Wright (2018) and V  rard (2019a) underscore the importance of bathymetry for circulation dynamics and anoxic extent. Notably, the presence of self-sustained oscillations in the Scot390M configuration emphasizes the nonlinear nature of the system's response to small changes in continental geometry. These results raise questions, similarly to Wong Hering et al. (2021), regarding the assessment of the reliability of different palaeogeographic reconstructions in the deep geological past. Our findings also reveal that continental configurations

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

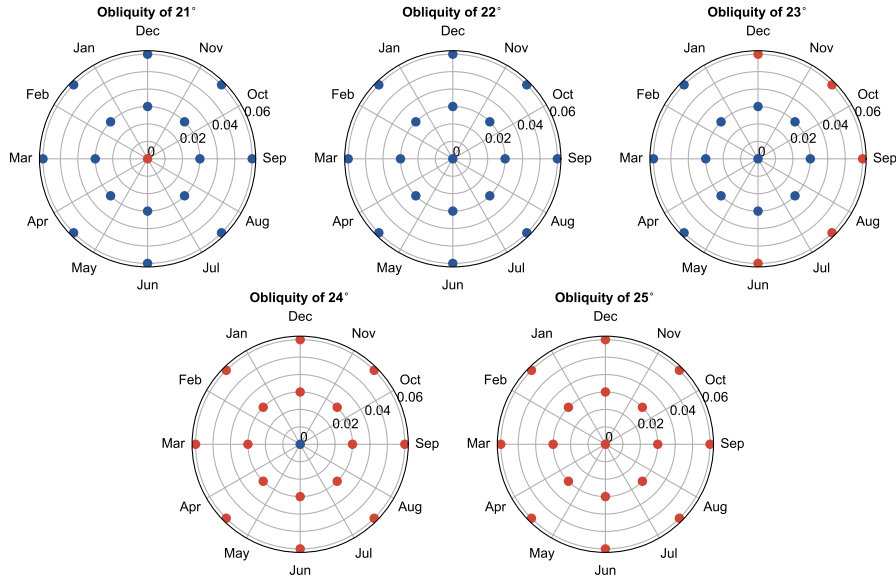


Fig. 2.12 Stable states and oscillatory regimes. Eccentricity–precession maps representing the nature of the solution of the system across a range of obliquity values: blue for stable oscillations and red for a stable steady state. Each dot represents a simulation conducted with a different astronomical configuration, where eccentricity is given by the radius and the longitude of perihelion by the angle on the circle (the corresponding month is provided as Jan: January, Feb: February, etc.). All simulations were performed for Scot390M using $2 \times p\text{CO}_2$, $1.25 \times [\text{PO}_4]$, and $0.7 \times p\text{O}_2$.

of the Middle and Late Devonian epochs are associated with increased OMZ extents (as opposed to those from the lower Devonian), thereby preconditioning the system for ocean anoxia. Therefore, in our experimental design, the continental configuration offers an explanation for the enhanced frequency of detected OAEs during these periods (see Fig. 22.13 in Becker et al., 2020). While our research identified continental configuration as an essential mechanism driving ocean $[\text{O}_2]$ in the Devonian, previous studies (modelling or geological outcomes) have reached similar conclusions for other periods. Donnadieu et al. (2016) investigated, using the Fast Ocean Atmosphere Model (FOAM), the Late Cretaceous climate and emphasized the potentially important role of palaeogeography as a preconditioning factor to the development of OAEs. Pohl et al. (2022) showed, with cGENIE, how continental rearrangements, even small, during the Phanerozoic eon led to profound variations in ocean oxygenation through reorganizations of large-scale ocean circulation. Recent studies on nitrogen proxies related to anoxia extent (Percival et al., 2022), along

with more accurate dating (Hedhli et al., 2023) of OAEs, have emphasized the importance of local factors. They suggest that the Hangenberg black shales do not represent a single global OAE but rather multiple, diachronous basins similar to the Black Sea, occurring around the world. To explain this, they propose that the tectonic configuration near the D–C boundary could have led to the creation of restricted marine basins, which in turn caused diachronous ocean anoxia associated with the Hangenberg extinction.

Then, we verified the profound yet straightforward effect of atmospheric pO_2 and global mean oceanic $[PO_4]$ on the benthic anoxic extent. As a general rule, both an increase in $[PO_4]$ and a decrease in atmospheric pO_2 lead to a greater extent of oceanic anoxia. This aligns with Percival et al. (2020), who propose that the upper Kellwasser, Annulata, and Hangenberg events were triggered by an influx of terrestrial nutrient from enhanced weathering. Our analysis also reveals that continental configuration substantially influences the amplitude and even sometimes the sign of the contribution of a pCO_2 increase to benthic $[O_2]$. This is due to the relative importance of two competing mechanisms: surface solubility loss and MOC strengthening. Studies generally suggest that OAEs of the Devonian occurred under warm conditions; however, some research indicates that these events could have also taken place during periods of a relatively cold global climate (Percival et al., 2020; Kabanov et al., 2023). Our results show that, depending on the continental configuration, both are valid hypotheses. Additionally, we identified a wide range of ocean dynamics with substantial effects on ocean $[O_2]$, including self-sustained oscillations, variations in overturning cell dominance, modification of sea ice cover, emergence of multistability, and prolonged ocean time response indicated by a hysteresis. These different behaviours are associated with substantial variations in global O_2 content. Hence, the richness of the ocean dynamics observed here may be relevant for understanding the dynamics of anoxia. For instance, the slow time response of the system under the gradual pCO_2 in the hysteresis simulation provides insight into the prolonged duration of certain OAEs. Applying constraints on atmospheric pCO_2 and surface temperature, such as those presented in Joachimski et al. (2009) and Becker et al. (2020), would help to better isolate the relevant ocean dynamics for individual events.

Finally, we assessed the role of astronomical forcing in driving variations in benthic anoxia through changes in large-scale ocean dynamics and O_2 solubility for different continental configurations. Obliquity consistently emerges as the

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

dominant orbital parameter influencing benthic ocean anoxia due to its effect on the annual mean temperature at high latitudes, where deep-ocean convection occurs. In our results, high obliquity systematically led to more extensive oxygen-depleted zones, with eccentricity and precession playing a secondary role. Several studies (Meyers et al., 2012; De Vleeschouwer et al., 2017; Da Silva et al., 2020) indicate that obliquity increases prior to the anoxic phases of Kellwasser events and OAE 2 (in the Late Cretaceous). The results also revealed that the continental configuration substantially modulates the influence of astronomical forcing on ocean anoxia. Additionally, astronomical forcing can shift the system's equilibrium, transitioning between stable oscillations and steady states, with obliquity and eccentricity being the primary determinants of these equilibrium states.

2.4.2 Model limitations

cGENIE belongs to the category of Earth system models of intermediate complexity. Its spatial resolution is coarse, the hydrological scheme is simplified, and the dynamics of atmospheric currents are not explicitly modelled. Reassuringly, cGENIE has repeatedly demonstrated its ability to capture large-scale ocean circulation patterns (Rahmstorf et al., 2005; Lunt et al., 2006; Cao et al., 2009; Marsh et al., 2013; Pohl et al., 2022), providing confidence in the robustness of the simulated global circulation (see Appendix A). Furthermore, even with its coarse spatial resolution, the model effectively captured the variations between continental reconstructions to produce very distinct ocean dynamics regimes. Yet, model limitations have some consequences regarding how we should interpret the implications of our results about the anoxia observed during the Devonian.

First, the phenomenon of multistability might have been exacerbated. It has long been suggested that multiple active oceanic circulation solutions may coexist with given boundary conditions, at least in somewhat idealized ocean geometries (Hughes and Weaver, 1994; Rahmstorf et al., 2005). However, authors have voiced the concern that more detailed coastline geometry, proper atmospheric feedbacks, and realistic atmospheric variability may, in the end, settle the system in one dominant regime. Nevertheless, considering the modelling work of Ferreira et al. (2011), Brunetti et al. (2019), Margazoglou et al. (2021), Eberhard et al. (2023), and Lohmann et al. (2024) as well as

theoretical considerations from Weijer et al. (2019), multistability and limit cycles remain plausible scenarios. Furthermore, as discussed in Pohl et al. (2022), Valdes et al. (2021) seem to obtain similar millennial oscillations in HadCM3 as those observed in this chapter.

Next, in its present configuration, cGENIE does not include ice sheet dynamics, with the implication that the sea level is constant. Ice sheets may also have grown to enough extent (De Vleeschouwer et al., 2015; Becker et al., 2020; Dahl et al., 2022) to release some water into the ocean, potentially impacting the circulation. Finally, cGENIE's resolution is too coarse to properly capture the connection between the deep ocean and epicontinental margins. Yet, the development of deep-ocean anoxia would help explain the synchronous character of anoxia observed in distant geological transects. However, the pathways by which deep-ocean anoxia may propagate into epicontinental seas or influence the conditions near arc islands require additional investigation.

Due to computational constraints and the extensive simulations required for each configuration, our study focused only on two distinct types of continental reconstructions. We would naturally encourage an investigation using a broader range of distinct continental configuration types. Additional insights may emerge by considering hybrid continental reconstructions, which would combine continental locations and shallow waters from Scotese and Wright (2018) with the deep ocean from V  rard (2019a). Such hybrid configurations were explored by Cerme  o et al. (2022), merging the continental reconstructions from Scotese and Wright (2018) and Merdith et al. (2021). To our knowledge, these approaches still remain largely unexplored, and we advocate for further investigations using different climate models, particularly EMIC and Coupled Model Intercomparison Project-class models, to elucidate similarities and potential disparities between cGENIE and finer models.

2.5 Conclusions

Using cGENIE, we carried out systematic sensitivity experiments to isolate the contributions of specific Devonian climate and palaeogeography components to ocean [O₂], providing new insights into Devonian OAEs. The key findings of this chapter can be summarized as follows.

2 | Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing

1. Continental configuration consistently modulates the signal of all other considered components of the Devonian climate (oceanic $[\text{PO}_4]$, atmospheric pO_2 , and pCO_2 as well as orbital forcing) on anoxia, highlighting its crucial contribution to OAEs. Furthermore, the continental configuration greatly influences ocean circulation and global O_2 content, with, at one point, the development of stable oceanic oscillations with periods ranging from 3000 to 5000 years. The oscillations, on average, are found to substantially reduce the $[\text{O}_2]$ in the deep ocean. The evolution of the continental configuration through the Devonian thus offers a plausible explanation for the enhanced frequency of reported OAEs during the Middle and Late Devonian periods by creating more extensive oxygen-depleted zones. Our investigation also revealed the presence of pronounced multistability (more than one stable state of the system exists for the same climatic configuration) for a specific continental configuration, providing a potential mechanism to account for the prolonged duration of these events (“lockdown” of the system in a state with strong oxygen-depleted conditions).
2. The influence of global mean oceanic $[\text{PO}_4]$ and atmospheric $[\text{O}_2]$ on ocean O_2 content is in line with current knowledge. Simulations indicate that both decreased atmospheric $[\text{O}_2]$ and increased oceanic $[\text{PO}_4]$ exacerbate ocean anoxia. The variation of atmospheric pCO_2 (here used as a climate forcing to modify temperatures) revealed important changes in ocean anoxia through modification of O_2 solubility, ocean circulation, and sea ice extent. The results indicate a range of ocean dynamics patterns, including stable oscillations, multiple convection cells, and hysteresis (dependence of the state of a system on its history), all highly sensitive to continental configuration. The hysteresis feature also provides a plausible mechanism to explain the prolonged duration of some OAEs. Furthermore, these processes and behaviours lead to important modifications of the ocean $[\text{O}_2]$, therefore strongly impacting the preconditioning of the ocean to anoxia.
3. Astronomical forcing substantially impacts ocean anoxia by altering ocean circulation and O_2 solubility. Obliquity consistently emerges as the primary orbital parameter driving the vast majority of observed oceanic O_2 variations due to its strong annual average influence on high latitudes. In our experiments, high obliquity persistently led to more extensive oxygen-depleted zones. Simulations demonstrate that

astronomical forcing can initiate stable oscillations within the system. The modulation of the orbital forcing impact on anoxia by continental configuration could explain why some OAEs correlate with astronomical cycles, whereas others do not, highlighting the temporal variability in the astronomical pacing of ocean anoxia throughout the Devonian.

This chapter underscores that shifts in ocean circulation, influenced by continental configuration, CO₂ levels, and orbital forcing, exert substantial impacts on ocean anoxia. Ocean circulation revealed surprisingly complex dynamics, with response times ranging from years to tens of thousands of years, which are relevant for understanding anoxia in the Devonian and, more generally, throughout the Phanerozoic. Our results also highlight the complexity of modelling Devonian OAEs and the fact that much work remains to reach complete comprehension of these critical episodes in Earth's history.

3

Spatially contrasted response of Devonian anoxia to astronomical forcing

3.1 Introduction

The objective of this chapter is to assess the impact of astronomical forcing on ocean anoxia, specifically through the modulation of continental nutrient fluxes, within a Late Devonian climate context. To this end, we performed transient simulations using cGENIE (Ridgwell et al., 2007), coupled offline with a continental weathering flux of nutrients. This flux is computed using an emulator trained on outputs from the general circulation model (GCM) HadSM3 (Valdes et al., 2017) and the geochemical model GEOCLIM (Maffre et al., 2025), as developed in Sablon et al. (2025). By incorporating a GCM, we account for the changes in precipitation and evaporation caused by astronomical forcing more accurately than with the standard version of cGENIE. In addition to improving the representation of hydrological responses, this approach further enhances the simulation of nutrient fluxes to the ocean, limited in the standard cGENIE model version due to its non-dimensional treatment of continental weathering (Colbourn et al., 2013). This modelling framework allows, on the

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

one hand, for a mechanistic assessment of how variations in orbital parameters (namely eccentricity, precession, and obliquity) affect terrestrial weathering rates and nutrient fluxes to the ocean, thereby influencing the development and spatial extent of anoxic conditions. On the other hand, the influence of astronomical forcing on $[O_2]$ through changes in ocean circulation is captured by cGENIE. A detailed description of the model configuration and experimental design is presented in Section 3.2. In Section 3.3.1, we examine the global characteristics of the transient coupled simulations, followed by a regional analysis in Section 3.3.2.

3.2 Methods

3.2.1 Models description

In the standard configuration of cGENIE, continental weathering is simply a function of the global mean continental temperature. This is inadequate to capture the effects of the astronomical forcing, as the latter primarily affects climate through changes in the spatial and seasonal distribution of incoming solar radiation (insolation). To address this, we replaced this simplified scheme with a state-of-the-art continental weathering module, which accounts for the coupled contributions of chemical weathering and erosion. Specifically, we used the framework described in Sablon et al. (2025) to couple cGENIE with a climate-weathering emulator. This emulator computes weathering fluxes under varying boundary conditions (orbital parameters and pCO_2) based on statistical relationships derived from outputs of HadCM3L, HadSM3 (the latter being the slab-ocean version of HadCM3) (Valdes et al., 2017), and GEOCLIM (used with fixed present-day average lithological fractions), explicitly accounting for the coupled contributions of chemical weathering and physical erosion to continental weathering. Both HadCM3L and HadSM3 were used, as the 81 HadSM3 simulations used to train the emulator required heat convergence flux data obtained from HadCM3L. The weathering fluxes are instantaneously routed from continental source cells to the closest ocean coastal grid cell via a nearest-neighbour scheme, which remains suitable given the similar grid layouts, both adapted from Scotese and Wright (2018), and the limited knowledge of the Late Devonian hydrological network. A detailed

overview of GEOCLIM’s continental weathering module is presented in Maffre et al. (2025), while a complete description of the emulator’s architecture, training process, and topography is documented in Sablon et al. (2025), the latter being repeated here for clarity (see Fig. 3.1).

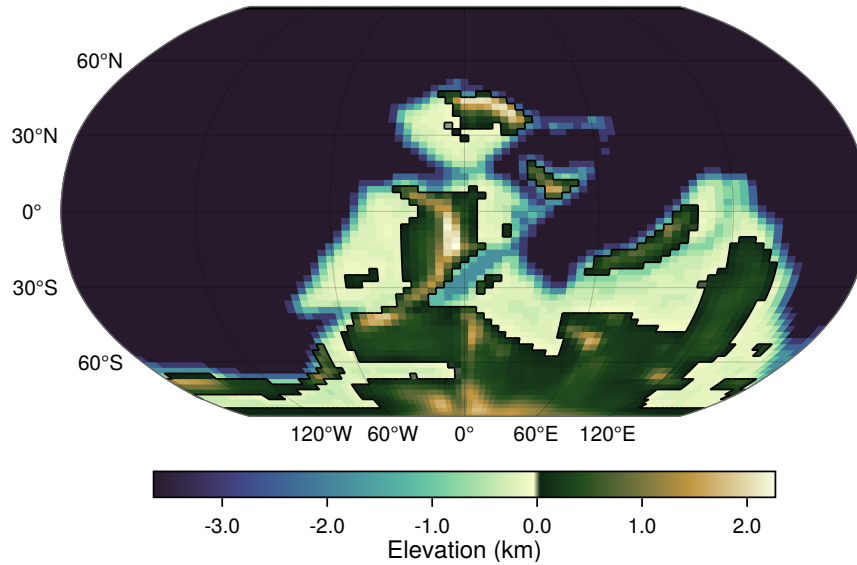


Fig. 3.1 Topography of the Late Devonian (370 Ma). Topography according to Scotese and Wright (2018), reproduced from Sablon et al. (2025). The bathymetry is identical to the one shown in Fig. 3.2b.

The coupling between the emulator and cGENIE is deliberately minimal and targeted, replacing the continental nutrient flux of PO_4 provided by cGENIE with values computed by the emulator. This replacement is performed offline every 1000 years, a frequency that is appropriate for capturing the long-term variability caused by the astronomical forcing. All other components and processes within the model remain unchanged, as our cGENIE setup uses a simplified, single-nutrient (PO_4) control on biological productivity (Ridgwell et al., 2007). In this configuration, biological productivity is driven by both $[\text{PO}_4]$ availability and local insolation. An increase in surface PO_4 availability stimulates biological productivity, thereby enhancing microbial O_2 consumption through remineralization in the water column. Moreover, limiting the coupling to a single flux ensures that other variables computed by ROKGEM remain unaffected, maintaining consistency and simplicity in the overall setup. As a result, cGENIE now responds to spatially-resolved,

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

astronomically-driven variations in continental PO_4 flux, thereby allowing a more robust investigation of the influence of orbital forcing on ocean anoxia.

In our simulations, the ocean is discretised on a 36×36 horizontal equal-area grid with 16 logarithmically spaced levels along the vertical (from 60 to 560 m). We use the continental configuration on which the emulator from Sablon et al. (2025) was trained, namely that of Scotese and Wright (2018), which represents the palaeogeography at 370 Ma (see Fig. 3.2). As this continental reconstruction was also used in Chapter 2, the large-scale ocean circulation patterns and associated diagnostics described there remain valid here; in particular, the overturning circulation shows only limited sensitivity to temperature changes (see Fig. 2.7c). Because the modelled climate system is older than the mid-Mesozoic advent of open-ocean planktic calcifiers (~ 200 Ma), the representation of calcium carbonate (CaCO_3) production is adapted accordingly (Ridgwell, 2005). Specifically, CaCO_3 production is restricted to shallow-marine CO_3 platforms, spatially constrained based on the reconstructions of Kiessling et al. (2003). The surface albedo and zonally averaged wind stress profiles are prescribed from the HadCM3L simulation of Sablon et al. (2025), conducted with the same pCO_2 (926 ppm) as in Valdes et al. (2021) and an orbital configuration characterized by an eccentricity of 0, a longitude of perihelion of 0° , and an obliquity of 23° . These fields are incorporated into cGENIE using the open-source “muffingen” suite v0.9.24 (Ridgwell, 2023), and are held constant throughout the transient simulation. The solar constant is set to 1325 W m^{-2} based on Gough (1981), less than today because this younger Sun was also weaker. The atmospheric $[\text{O}_2]$ is set to 80 % of its present-day value to reflect the lower levels characteristic of the Late Devonian (Krause et al., 2018; Mills et al., 2023). The estimated climate sensitivity of cGENIE is $\sim 3^\circ\text{C}$ per doubling of pCO_2 , which is close to the mean value from the CMIP5 and slightly lower than that from CMIP6 (Zelinka et al., 2020). Ocean and atmosphere parameter values follow the standard cGENIE setup of Cao et al. (2009) and are identical to those in Pohl et al. (2022) and in Chapter 2. In our setup, the empirical equation proposed by Dunne et al. (2007) represents C_{org} burial in marine sediments, while the empirical parameterization of Wallmann (2010) accounts for redox-dependent regeneration of P from sediments. Following Dunne et al. (2007), C_{org} burial scales with the flux of organic matter reaching the seafloor and is therefore a function of surface ocean productivity. Following Wallmann (2010), a substantial portion of P initially bound in organic matter is degraded in surface sediments and released

into the ocean as dissolved PO_4 . Furthermore, PO_4 release from sediments is enhanced under low O_2 conditions in line with observations (Ingall and Jahnke, 1994). A detailed description of these schemes and their implementation in cGENIE is provided in Hülse and Ridgwell (2025).

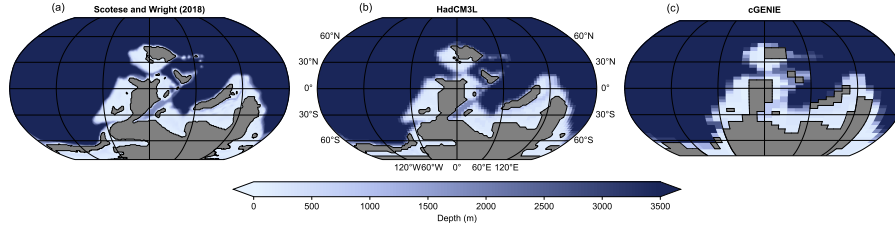


Fig. 3.2 Late Devonian (370 Ma) bathymetry. Comparison between (a) the continental reconstruction from Scotese and Wright (2018), (b) the same reconstruction interpolated onto the HadCM3L model grid used in the emulator and (c) as per (b) on the cGENIE grid.

3.2.2 Experimental setup

The astronomical forcing for the Devonian is not known precisely, due to the chaotic nature of the Solar System and the subtle, yet cumulative, effects of tidal dissipation on axial precession (Laskar et al., 2011). A series of plausible solutions is now available (Zeebe and Lantink, 2024), but our experiment design was finalised before that publication appeared. Nevertheless, the astronomical solution employed here shares the same frequency content and amplitude-modulation structure as those found across the Zeebe–Lantink ensemble. We adopted the same hybrid approach as Sablon et al. (2025). It relies, for planetary motion, on the solution by Laskar et al. (2011) (La11a), from which we extracted the interval between 123.3 Ma and 122.2 Ma. This interval features a resonance between the 2.4 Myr eccentricity period (associated with the g_4 – g_3 terms) and the 1.2 Myr obliquity modulation (associated with the s_4 – s_3 terms), as in most of the Cenozoic. This resonance is characterised by an increase in obliquity variance when eccentricity reaches a 2.4 Myr node, at which point its variance is lowest and the 100 kyr component of the eccentricity signal disappears. The node occurs approximately midway through the selected interval.

We coupled this solution with the precession model of Sharaf and Boudnikova (1967), following the procedure outlined in Berger and Loutre (1991). This involves first performing a harmonic decomposition of the planetary

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

solution (using R code based on Šidlichovský and Nesvorný, 1996), and then specifying a reference obliquity and general precession rate. These reference values are given by Farhat et al. (2022) for the period around 370 Ma. With this construction, the solution yields obliquity frequencies of 30 555 and 37 335 years, and climatic precession frequencies of 16 470 and 19 386 years, which are considered plausible for the Late Devonian. The R code used to generate these time series is available in Crucifix (2025). We verified that the time series of obliquity and longitude of perihelion are nearly identical to those obtained by integrating, forward in time, the precession model of Laskar and Robutel (1993) with an appropriate Earth–Moon distance and dynamical ellipticity. The latter approach is admittedly more straightforward, but was not integrated into our workflow at the time the experiment was prepared.

The length and choice of this specific astronomical solution reflect a compromise between representativeness and computational feasibility, given that a 1.1 Myr simulation with cGENIE requires two months of continuous computation on our systems. In particular, we cannot know whether the (g_4 – g_3) versus (s_4 – s_3) resonance was active during the Devonian, but previous cyclostratigraphic interpretations assumed a well-expressed 2.4 Myr eccentricity node and pronounced obliquity cycles when crossing the node (De Vleeschouwer et al., 2017). The chosen solution satisfies these assumptions. Moreover, it conveniently includes within a single sequence a transition from well-expressed 100 kyr eccentricity cycles modulated by a 405 kyr cycle, to the 2.4 Myr node (during which the 100 kyr cycles disappear), and then back to well-expressed 100 kyr eccentricity cycles. For reference, we use the heliocentric convention for expressing the longitude of perihelion, which is therefore 0° when perihelion occurs in September (as in Sablon et al., 2025).

cGENIE reached equilibrium through a two-step spin-up process similar to Ridgwell and Hargreaves (2007), Hülse and Ridgwell (2025) and Vervoort et al. (2024). In the initial spin-up phase (SPIN1), ocean dynamics and biogeochemical cycling equilibrate with fixed atmospheric $p\text{CO}_2$ and $\delta^{13}\text{C}$ under a closed system. Burial of CaCO_3 , C_{org} , and P are balanced by global weathering inputs, and the resulting data are used to determine global equilibrium burial rates. The second spin-up phase (SPIN2) uses an open-system setup, with weathering fluxes set to the equilibrium with burial rates from SPIN1 and allowed to respond to temperature. A complete description of this two-step procedure in cGENIE, including C_{org} and P feedbacks, is detailed in Hülse and Ridgwell (2025). We found that during the SPIN2, the model exhibited

substantial drift, most notably in $p\text{CO}_2$, with the system requiring up to 500 kyr to reach equilibrium. To address this, we heuristically adjusted the initial $p\text{CO}_2$ in SPIN1 to guide the model toward a geochemically consistent Late Devonian state. Part of this consistency has already been achieved by estimating the initial mean $[\text{PO}_4]$ based on outputs from GEOCLIM. By the end of SPIN2, the system reached an atmospheric $p\text{CO}_2$ of ~ 550 ppm, consistent with the estimates of Chen et al. (2021) and Dahl et al. (2022), and an average surface $[\text{PO}_4]$ of $0.47 \mu\text{mol kg}^{-1}$, in agreement with Sharoni and Halevy (2023). Furthermore, the system achieved modern-like burial fluxes (similar to Hülse and Ridgwell, 2025), including $0.144 \text{ PgC yr}^{-1}$ of CaCO_3 (reef only) (Frankignoulle and Gattuso, 1993), $0.075 \text{ PgC yr}^{-1}$ of C_{org} (Dunne et al., 2007; Bradley et al., 2022), and $0.062 \text{ Tmol yr}^{-1}$ of P (Benitez-Nelson, 2000; Ruttenberg, 2003). The cause of this drift remains unclear, but our testing suggests a role of seasonal variability amplification under specific continental geometries. Specifically, continental configurations symmetric about the equator generally exhibit no model drift, highlighting the influence of continental geometry. A full investigation of the origin of this drift lies beyond the scope of this chapter, as it would require substantial computational time, with a 500 kyr simulation requiring roughly one month of runtime.

Starting from the equilibrium state (SPIN2), the continental PO_4 nutrient flux provided by cGENIE is replaced with values computed by the emulator. The model is then run for an additional 100 kyr (SPIN3) with astronomical parameters fixed at their average value across the adopted astronomical solution, allowing the system to adjust to the new PO_4 flux boundary condition. This average astronomical configuration is characterised by an eccentricity of 0.027, an obliquity of 0.388 rad (22.23°) (Farhat et al., 2022) and longitude of perihelion set to 90° ($\sin \varpi = 1$). To ensure continuity, the global average flux of PO_4 computed by the emulator is rescaled (decreased by $\sim 10\%$) to perfectly align with the global average flux of PO_4 computed by the built-in weathering module of cGENIE at the end of SPIN2. Following this adaptation period, a series of 3 transient simulations spanning the full 1.1 Myr astronomical solution were conducted. These include: (1) a run with all astronomical parameters evolving (Full); (2) a sensitivity experiment with only obliquity varying while eccentricity and precession were held constant at their average values (Obli); (3) a run in which only eccentricity and precession vary, with obliquity fixed at its average value (Ecc-prec). Simulations description is summarized in Table

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

3.1. Additionally, a control simulation was performed in which all astronomical parameters were held constant at their mean values.

Name	Type	Emulator	Duration (kyr)	IC	Forcings	BC
SPIN1	Closed	Off	20	—	pCO ₂ ; pO ₂ ; surface flux of DIC and ALK	Constant wind fields and albedo profile (HadCM3L)
SPIN2	Open	Off	500	SPIN1	pO ₂	as in SPIN1
SPIN3	Open	On	100	SPIN2	pO ₂	as in SPIN1
Full	Open	On	1100	SPIN3	pO ₂	as in SPIN1
Obli	Open	On	1100	SPIN3	pO ₂	as in SPIN1
Ecc-prec	Open	On	1100	SPIN3	pO ₂	as in SPIN1

Table 3.1 Experimental design. The type indicates whether the model operates in a closed or open configuration, with the closed setup meaning that every chemical species lost through sedimentation is compensated by an equivalent input from weathering. The emulator is the one from Sablon et al. (2025) that is built on model outputs from HadCM3L, HadSM3, and GEOCLIM. Initial conditions (IC) for SPIN1 are derived from GEOCLIM simulations and include PO₄, alkalinity (ALK), calcium, and sulfate. Forcings correspond to quantities that are explicitly prescribed during the simulations and are the same as in Hülse and Ridgwell (2025). Boundary conditions (BC) are derived from HadCM3L simulations as described in Valdes et al. (2021).

3.3 Results

3.3.1 Moderate global astronomical influence

The global time series of atmospheric pCO₂, oceanic [PO₄] and [O₂] for each transient simulation conducted across the astronomical solution are shown in Fig. 3.3. Throughout the reference simulation with all astronomical parameters evolving (black line in Fig. 3.3), atmospheric pCO₂ fluctuates by up to 40 ppm around a mean value of 555 ppm, driven by interactions within the open C cycle (ROKGEN and C_{org} burial). In the ocean, globally-averaged [PO₄] varies by ~0.1 μmol kg⁻¹ around a mean of 2.67 μmol kg⁻¹, while global mean [O₂] remains within a range of 5 μmol kg⁻¹ around an average of 54 μmol kg⁻¹ (see Appendix C.1). The temporal variability of both atmospheric pCO₂ and oceanic [PO₄] is almost exclusively driven by the combined forcings of eccentricity and precession, with obliquity playing a very minor role (see Fig. 3.3a and b). Overall, variations in global mean concentrations caused by astronomical forcing remain of moderate amplitude. This is consistent with the results of Sablon et al. (2025) and unsurprising considering that global averages can

mask spatially heterogeneous responses, including contrasting and potentially compensating regional signals.

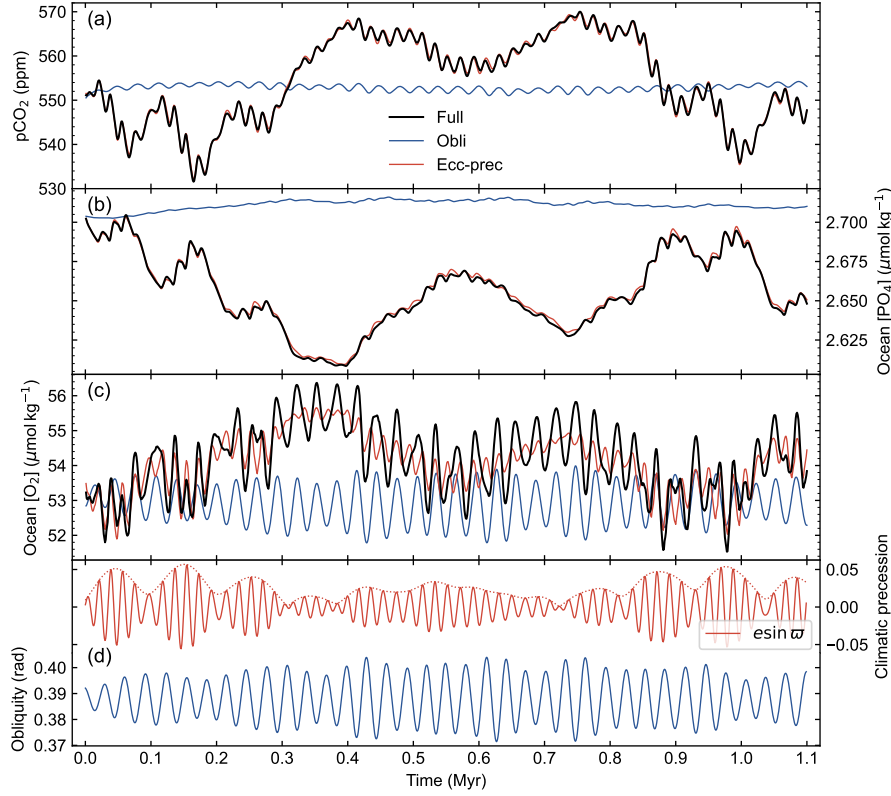


Fig. 3.3 Global response to astronomical forcing. Global time series of (a) $p\text{CO}_2$, ocean (b) $[\text{PO}_4]$ and (c) $[\text{O}_2]$. The black curve represents the simulation in which all astronomical parameters evolve. The blue curve represents the simulation with only obliquity varying, while the red curve corresponds to the simulation where only eccentricity and precession evolve. (d) The astronomical solution used in the simulations, with eccentricity in dotted red, climatic precession in red and obliquity in blue. Here, e denotes the eccentricity, and ϖ represents the longitude of perihelion.

Atmospheric $p\text{CO}_2$ and oceanic $[\text{PO}_4]$ evolve in anti-phase throughout the simulation (see black and red curves in Fig. 3.3a and b). This inverse relationship occurs because intensified weathering simultaneously enhances CO_2 consumption and increases the continental flux of PO_4 to the ocean, leading to lower atmospheric $p\text{CO}_2$ and higher oceanic $[\text{PO}_4]$. The dominant control of eccentricity and precession on atmospheric $p\text{CO}_2$ and oceanic $[\text{PO}_4]$ arises from their pronounced effect on continental weathering fluxes. Specifically, these two orbital parameters can drive changes in PO_4 delivery

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

to the ocean of up to 9.5 %, compared to only ~ 1.5 % under obliquity-driven forcing alone. When all three orbital parameters evolve simultaneously, this modulation can reach 10.5 %. In our simulations, the dominant driver is the precession-sensitive monsoon system captured by the emulator: precession alters monsoon intensity and distribution, which directly modulates the spatial pattern of runoff and thus weathering and PO_4 delivery. Beyond this, eccentricity is positively correlated with PO_4 weathering, such that periods of high eccentricity are associated with enhanced oceanic $[\text{PO}_4]$, a feature already identified and documented in Sablon et al. (2025).

A global low O_2 state characterises the ocean in these simulations (see Fig. 3.3c) compared to the modern climate (Schmidtke et al., 2017; Garcia et al., 2024), consistent with the findings of Chapter 2 under similar boundary conditions and the estimations made by Tostevin and Mills (2020) based on long-term geochemical proxy data. While all three orbital parameters affect global-mean $[\text{O}_2]$, they operate through distinct mechanisms. Eccentricity and precession primarily influence global $[\text{O}_2]$ by modulating the oceanic PO_4 inventory. The relationship between globally-averaged $[\text{PO}_4]$ and $[\text{O}_2]$ is evidenced by a strong correlation ($R^2 = 0.82$ and $p\text{-value} = 0.016$)¹ between the two red curves in Fig. 3.3b and c. These $[\text{PO}_4]$ variations arise from changes in the continental weathering flux of PO_4 , with high eccentricity associated with reduced global $[\text{O}_2]$. In contrast, obliquity exerts only a very weak effect on global $[\text{PO}_4]$ that is insufficient to explain the simulated $[\text{O}_2]$ variations. This is reflected by the almost absent correlation ($R^2 = 0.06$ and $p\text{-value} = 0.467$) between the two blue curves in Fig. 3.3b and c. Instead, obliquity primarily influences global $[\text{O}_2]$ through its strong modulation of high-latitude insolation, as also noted in Chapter 2. Because modelled biological productivity explicitly depends on local insolation (Ridgwell et al., 2007), obliquity substantially alters O_2 consumption in these regions. These variations lead to changes in subsurface (around 60–130 m depth) $[\text{O}_2]$ of up to $4 \mu\text{mol kg}^{-1}$. As these $[\text{O}_2]$ anomalies emerge in deep-water formation zones, they are efficiently distributed throughout the global ocean via large-scale overturning circulation, resulting in consistent O_2 variations of $\sim 4 \mu\text{mol kg}^{-1}$ across the benthic ocean (not shown). Consequently, times of high obliquity are associated with decreased global $[\text{O}_2]$, driven by increased biological productivity in high-

¹All presented statistics account for the temporal autocorrelation inherent in our setup, using an effective sample size correction based on the N_{eff} method, following the approach of Bretherton et al. (1999).

latitude regions. There, the productivity anomalies driven by obliquity are more than three times larger than those caused by eccentricity and precession combined. Hence, the combination of high eccentricity and high obliquity results in the most severe depletion of simulated global $[O_2]$ (see Fig. 3.3c and d).

3.3.2 High regional variability

To assess regional expressions of $[O_2]$ variability driven by astronomical forcing, we defined distinct regions, as shown together with their associated watersheds in Fig. 3.4a and b. They are named after their approximate paleogeographic positions: region SA (South America), region WL (western Laurussia), region Si (Siberia), region NP (northern pole), and region LG (Laurussia–Gondwana). These regions were initially constrained by the depth distribution of Devonian anoxia proxy data, which predominantly originates from shallow-marine settings. Because the ocean floor from the Devonian period has been lost to subduction and plate tectonic processes, proxies for deep-water properties are scarce (Granot, 2016; Scotese and Wright, 2018). Consequently, grid cells deeper than 1000 m were excluded, except for those associated with deep-water formation, which occurs in regions SA and NP. Within this depth-limited framework, we further refined the regions by grouping model grid points based on the temporal variance of $[PO_4]$ and $[O_2]$ (see Appendix C.2), with the final result shown in Fig. 3.4a. Hence, this approach enables us to assess whether astronomical forcing triggers distinct biogeochemical responses across various regions.

Fig. 3.4c displays the time series of regionally-averaged $[O_2]$ and anoxic volume anomalies, for each region (as defined in Fig. 3.4a), in the reference simulation with all astronomical parameters evolving concurrently (Full). The results highlight a marked spatial heterogeneity in the biogeochemical response to astronomical forcing. On the one hand, regions SA and LG exhibit strong sensitivity to astronomical variability. In these regions, $[O_2]$ fluctuates by 45 and 19.5 $\mu\text{mol kg}^{-1}$, respectively, equivalent to a 35 % deviation from their regional means. Simulated $[O_2]$ reaches its lowest values during periods of maximum eccentricity. These pronounced O_2 variations translate into substantial changes in anoxic volume, reaching $\sim 19\%$ in region SA and 13.5 % in region LG. On the other hand, region Si is mostly unaffected by astronomical

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

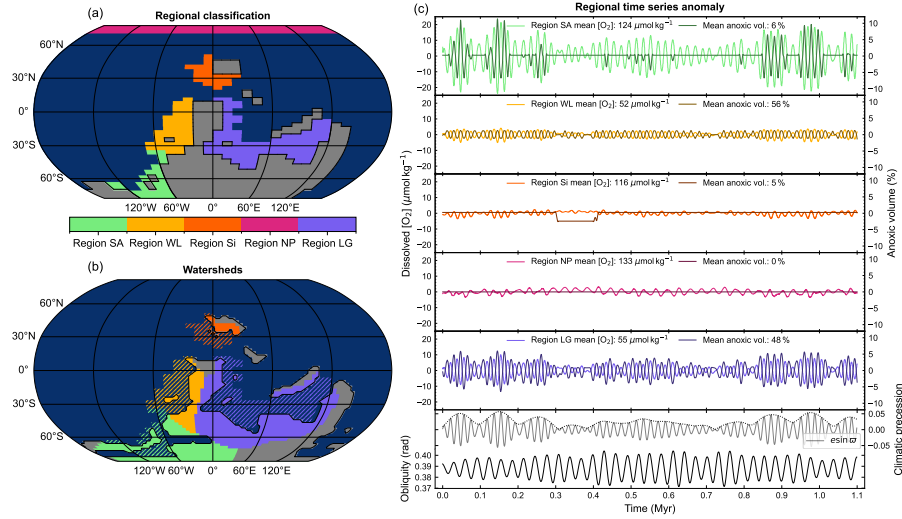


Fig. 3.4 Regional variation of $[O_2]$ and anoxia. (a) Definition of the five regions. (b) Watersheds based on the nearest-neighbour continental runoff routing scheme. The colour of the continental grid cell indicates in which region the weathering flux of PO_4 computed by the emulator of Sablon et al. (2025) is routed. The hashed areas represent the regions as defined in cGENIE and are the same as in panel (a). The discrepancies between the watersheds and the regions arise from the different grid resolution of cGENIE and HadSM3. (c) Time series of average oceanic $[O_2]$ anomalies and anoxic volume anomalies (in %) for each region. These quantities were computed over the full extent of each region, from the second vertical layer down to ~ 1000 m depth, excluding the surface layer as it is in equilibrium with the atmosphere. The anoxic volume is shown in a darker colour, and the anomaly is expressed as a difference of %. The anoxic threshold is set at $6.5 \mu\text{mol kg}^{-1}$ after Sarr et al. (2022). For both $[O_2]$ and anoxic volume, the y-axis scales are identical across all regional panels to allow direct comparison. As in Fig. 3.3, the bottom panel displays the astronomical forcing, but shown in black for clarity.

forcing. Temporal variability in both $[O_2]$ and anoxic volume is limited to $\sim 5\%$ and 2.5% , respectively, with the anoxic volume remaining stable throughout most of the simulation. Although the signal is subtle in magnitude, region Si exhibits an opposite precession phasing compared to regions SA and LG, a feature resulting from their locations in different hemispheres. Region NP exhibits no anoxic conditions over the period, because of its consistently high $[O_2]$ and the limited magnitude of $[O_2]$ variations, which are insufficient for any grid cell in the region to cross the anoxic threshold. These high $[O_2]$ values over region NP are expected given the presence of major deep water formation in this region, whereas the relatively weaker deep water formation

in region SA explains why this region can exhibit anoxia (see Fig. C.1e and Fig. C.2).

The relative influence of individual astronomical parameters is clarified by the power spectrum analysis of the $[O_2]$ time series (Fig. 3.5). Precession emerges as the dominant driver of $[O_2]$ variability in regions SA, WL, Si, and LG, while $[O_2]$ in region NP is primarily shaped by obliquity. Although eccentricity produces no distinct spectral peak, it remains essential through its modulation of precession amplitude (see Fig. 3.4c). Notably, periods of high eccentricity tend to coincide with decreased $[O_2]$ across all regions, underscoring its consistent impact.

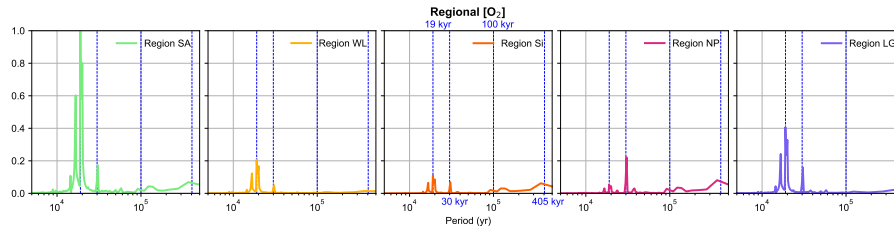


Fig. 3.5 *Normalized Fourier power spectrum of the regional $[O_2]$ time series. Vertical dashed lines indicate the characteristic periods of the astronomical parameters: 19 kyr for precession, 30 kyr for obliquity, and 100 kyr and 405 kyr for eccentricity.*

By definition, variations in anoxic volume arise from changes in regional $[O_2]$. Typically, these $[O_2]$ fluctuations are closely tied to changes in biological productivity and subsequent remineralization. In regions SA, WL, and LG, $[O_2]$ variability is almost entirely driven by variations in the $[PO_4]$ component of biological productivity (regional $R^2 \geq 0.75$ and p-values $< 10^{-3}$). In region NP, $[O_2]$ variability aligns closely with the insolation component of biological productivity ($R^2 = 0.66$ and p-value $< 10^{-3}$), whereas the $[PO_4]$ component shows no meaningful relationship ($R^2 = 0.01$, p-value = 0.63). This indicates that insolation-forced biological productivity, rather than $[PO_4]$, controls $[O_2]$ dynamics in this region. Region Si exhibits a distinct behaviour compared with all others. It is the only region where $[O_2]$ variability is not primarily driven by biological productivity ($R^2 = 0.22$ and p-value $< 10^{-3}$), indicating the dominance of another mechanism. The strong correspondence between $[O_2]$ in region Si and the northern hemisphere mean ($R^2 = 0.79$, p-value $< 10^{-3}$) suggests that large-scale physical transport and mixing, consistent with strong currents and circulation in this region (see Fig. 3.7), drive these regional $[O_2]$ fluctuations. Overall, our results indicate that when regional $[O_2]$ variability is high, it is

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

primarily driven by the $[\text{PO}_4]$ component of biological productivity. However, when $[\text{PO}_4]$ fluctuations are limited, other processes, such as insolation-forced changes in biological productivity or large-scale advection and mixing, become more critical.

With the link between $[\text{PO}_4]$ and $[\text{O}_2]$ established, we now turn to the drivers of $[\text{PO}_4]$ variability. Figure 3.6 shows the time series of average $[\text{PO}_4]$ and PO_4 weathering, in addition to the linear regression between these two quantities for each region. Region NP has been excluded because there is no direct regional weathering flux of PO_4 coming from the continents. For correlation analysis, the $[\text{PO}_4]$ time series for each region (except region Si) was slightly shifted to best align with the weathering time series. This adjustment accounts for the natural time lag between the two quantities, as $[\text{PO}_4]$ typically increases when the weathering flux of PO_4 is high. Namely, even as continental weathering begins to decrease, $[\text{PO}_4]$ continues to rise as long as the PO_4 input to a given region temporarily exceeds the rate at which it is consumed, producing a lag of several thousand years between the weathering signal and the $[\text{PO}_4]$ response (see Fig. 3.6). To ensure the mechanism remains consistent with an astronomical-forcing interpretation, this lag was chosen to maximize the correlation but was limited to a maximum of 5 kyr (approximately one-fourth of a precession cycle). Because both the magnitude of the PO_4 weathering peak and the rate at which PO_4 is consumed through biological productivity differ across regions, the resulting lag is region-specific. When a negative lag is applied to $[\text{PO}_4]$ in regions SA, WL, and LG, it becomes clear that regional weathering accounts for most of the variations in $[\text{PO}_4]$. Hence, in these regions, variations in $[\text{O}_2]$ and anoxic extent are predominantly driven by regional $[\text{PO}_4]$, hence PO_4 weathering, which in turn is mainly modulated by eccentricity and precession (see Fig. 3.6).

In region Si, the relationship between $[\text{PO}_4]$ and PO_4 weathering differs fundamentally from that of all other regions. Unlike SA, WL, and LG, where regional PO_4 weathering clearly imprints on $[\text{PO}_4]$, no meaningful correspondence emerges in region Si. The regional PO_4 weathering flux is comparatively weak (about half that of region LG), and strong currents promote rapid advection and mixing, preventing local accumulation of weathered PO_4 (see Fig. 3.7). As a result, regional $[\text{PO}_4]$ variations do not reflect local weathering input. Instead, $[\text{PO}_4]$ in region Si closely follows the broader Northern Hemisphere signal ($R^2 = 0.98$ and $p\text{-value} < 10^{-3}$), indicating that large-scale transport governs its temporal evolution. This behaviour is consistent with

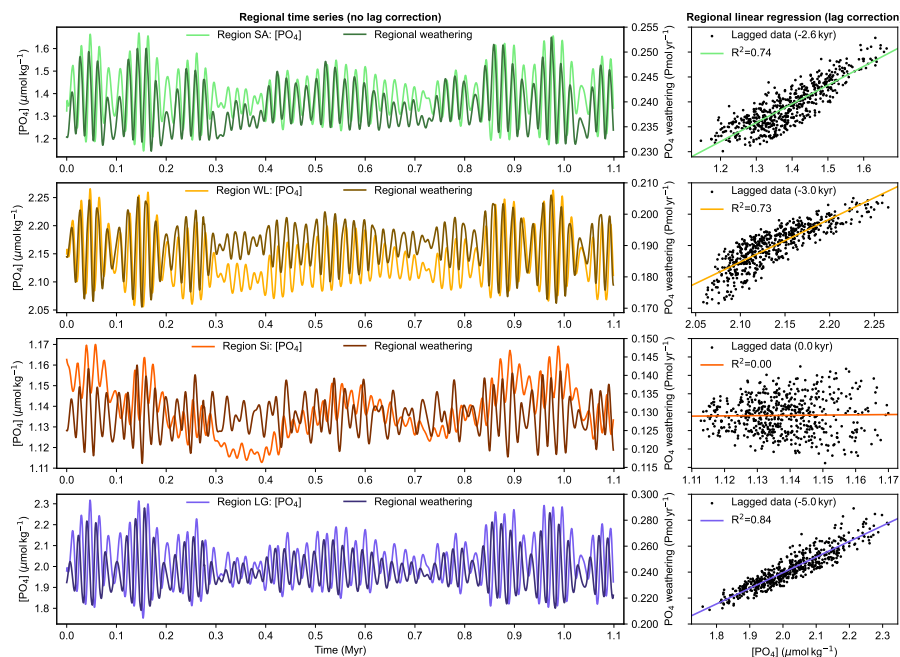


Fig. 3.6 *Linking continental PO_4 weathering flux and regional $[PO_4]$. Displayed are correlations between regional $[PO_4]$ and their corresponding regional weathering fluxes. A negative time lag is applied in the figures on the right, where the regression is computed, and is absent from the figures on the left. Regions SA, WL, and LG have all p -values smaller than 10^{-3} , while region Si has a p -value of 0.35. Region NP is excluded from the analysis due to the absence of direct continental PO_4 weathering.*

the mechanism identified earlier: circulation and mixing dominate both $[O_2]$ and $[PO_4]$ variability in region Si.

3.4 Discussion

3.4.1 Implications

We used cGENIE with an upgraded representation of weathering taken from Sablon et al. (2025), to investigate the influence of astronomical forcing on Late Devonian ocean oxygenation. Our simulations indicate that the Late Devonian background state was already characterised by low oceanic $[O_2]$, which likely contributed to the increased frequency of OAEs observed throughout this

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

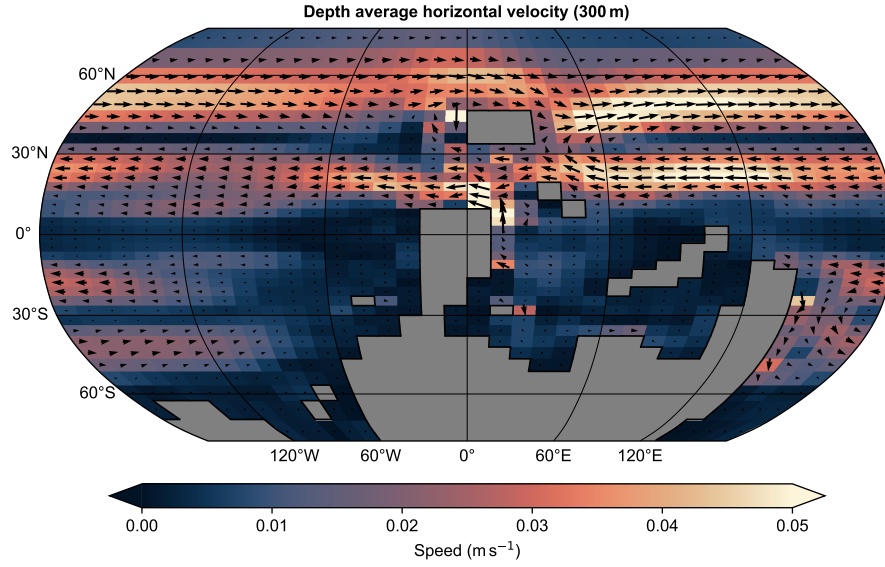


Fig. 3.7 Surface ocean circulation. Mean horizontal ocean velocity (m s^{-1}) averaged over the upper 300 m. Arrow direction indicates flow orientation, while arrow length is proportional to velocity magnitude (also represented with background shading).

period (Becker et al., 2020). We found that astronomical forcing leaves a discernible imprint on the global time series of atmospheric pCO_2 , oceanic $[\text{PO}_4]$, and $[\text{O}_2]$. Notably, the evolution of atmospheric pCO_2 under astronomical forcing closely mirrors the results reported by Sablon et al. (2025), exhibiting a similar amplitude of ~ 40 ppm, with higher atmospheric pCO_2 corresponding to periods of minimum eccentricity. A similar pCO_2 range was also obtained by Vervoort et al. (2024) when running cGENIE with astronomical forcing, using a very different experimental setup featuring an idealized continental configuration and no representation of C_{org} burial. In our simulations, $[\text{O}_2]$ variations primarily occur through the influence of eccentricity and precession on continental weathering fluxes, as well as obliquity on high-latitude biological productivity. Periods of combined high eccentricity and high obliquity produce the most pronounced deoxygenation, although global mean $[\text{O}_2]$ variations remain within a modest magnitude range of $5 \mu\text{mol kg}^{-1}$ throughout the simulations. Because the ocean exhibits substantial spatial heterogeneity in benthic $[\text{O}_2]$, with differences reaching $100 \mu\text{mol kg}^{-1}$, it is unlikely for the simulated $[\text{O}_2]$ variations to drive global-scale benthic areas below the anoxia threshold. Based on our modelling, it is thus highly implausible that

the astronomical forcing alone could induce an OAE over the entire global ocean (i.e., including the benthic ocean).

Building on the global-scale analysis, we performed a more localized investigation by defining specific regions to capture potentially distinct biogeochemical dynamics induced by astronomical forcing. The results reveal that eccentricity maxima commonly coincide with the most pronounced anoxic extent, supporting the proposal by Ma et al. (2022) and Huygh et al. (2025) that the Upper Kellwasser coincides with an eccentricity maxima configuration. However, both the magnitude and the dominant astronomical parameter driving this response vary markedly across regions, underscoring the spatial heterogeneity captured in our simulations. While certain regions exhibit strong sensitivity to astronomical forcing, with $[O_2]$ varying by up to 35 % and the anoxic volume by up to 19 %, others remain largely unaffected. Regions near continental margins (i.e., more directly influenced by weathering fluxes) exhibit a strong precessional control, with the largest variations in $[O_2]$ and anoxic volume occurring in these weathering-dominated settings. This influence is not limited to low-latitude areas; for instance, region SA exhibits a notable precession signal despite its relatively high latitude, whereas precession is generally thought to primarily affect low latitudes due to its strong control on precipitation patterns (De Vleeschouwer et al., 2012). In contrast, high-latitude regions far from continental margins (i.e., less directly influenced by weathering fluxes) are more sensitive to obliquity-driven changes, particularly through their influence on the insolation component of biological productivity. These findings underscore the pivotal role of PO_4 weathering and biological productivity in shaping regional biogeochemical responses, aligning with the “top-down” hypothesis proposed in Carmichael et al. (2019). However, physical processes such as ocean circulation and tracer advection can override this control, as exemplified in region Si, where local $[O_2]$ and $[PO_4]$ dynamics are decoupled from regional weathering due to strong transport. Our results further demonstrate how regions SA, WL, and LG, characterized by relatively weak surface circulation, provide ideal conditions for astronomically-driven weathering variations to leave a substantial imprint on local $[O_2]$.

Altogether, these results demonstrate that astronomical forcing can exert pronounced control on ocean biogeochemistry, with its impact shaped by local physical conditions. Furthermore, the regional analysis of the shallow ocean suggests that an astronomical signal may appear globally distributed across the observational record. However, it also indicates that proxy records

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

from distinct locations may reflect fundamentally different expressions of an astronomical signal, potentially leading to contrasting interpretations of its role in driving ocean anoxia.

Despite the important contribution that astronomical forcing can exert on $[O_2]$, the biogeochemical response of the system remains relatively simple when compared to the forcing. Specifically, the regions often exhibit a quasi-linear response to the forcing, lacking clear signs of long-term memory effects or strong non-linearities. This is particularly surprising given that redox-dependent P regeneration is represented in our model configuration (using the scheme from Wallmann, 2010), a feature explicitly proposed in Percival et al. (2020) to explain the sustainability of Late Devonian anoxia based on the investigation of sedimentary concentrations. Hence, the absence of prolonged anoxia in our simulations indicates that the PO_4 variations induced by astronomical forcing may be either too gradual or too limited in amplitude to trigger or maintain an anoxic state over extended timescales in our experimental setup (e.g., 10^5 years). Our results also suggest that OAEs could manifest as a series of smaller, short-lived, precession-paced episodes (see Fig. 3.4c and supplementary video, Gérard, 2026) rather than a single, prolonged global event, similar to the scenario proposed by Hedhli et al. (2023). These findings motivate future studies centred on additional processes that may influence the system response, including vegetation–climate interactions driven by orbital forcing and the effects of large, episodic nutrient inputs. In particular, assessing the persistence and biogeochemical consequences of such perturbations could help constrain the conditions under which sustained anoxia might emerge.

3.4.2 Limitations

Because cGENIE is a relatively simple model, it suffers from well-known intrinsic limitations. Among these are its coarse spatial resolution, resulting in a simplified representation of continental geometry and shallow-marine environments, the absence of explicitly resolved atmospheric dynamics, a basic hydrological scheme, and the lack of ice-sheet dynamics. Nevertheless, cGENIE has been widely used in previous studies and has demonstrated its capacity to reproduce large-scale ocean circulation features (Rahmstorf et al., 2005; Lunt et al., 2006; Cao et al., 2009; Marsh et al., 2013; Pohl et al., 2022; Laridon et al., 2025) and to accurately simulate key aspects of ocean biogeochemistry (Ridgwell

et al., 2007; Ridgwell and Hargreaves, 2007; Colbourn et al., 2013; Ward et al., 2018; Adloff et al., 2020; Reinhard et al., 2020; Crichton et al., 2021; Van De Velde et al., 2021; Naidoo-Bagwell et al., 2024; Stappard et al., 2025). These studies collectively demonstrate the model's reliability in simulating paleoclimate conditions and associated biogeochemical responses. Furthermore, some of these limitations are addressed by our specific experimental design. The prescribed wind stress field, although not responsive to climate variability, was derived from HadCM3L simulations conducted by Sablon et al. (2025). More generally, the emulator accounts for changes in precipitation associated with variations in astronomical configuration and atmospheric $p\text{CO}_2$, thereby improving the representation of hydrological controls on PO_4 weathering. Together, these features enable a more realistic representation of two central climate components in our study: PO_4 weathering and ocean circulation.

Still, several important limitations of our approach carry implications for interpreting the results. Our results could depend on the selected paleogeographic reconstruction, given the substantial uncertainties that persist in deep-time topography and, by extension, in slope, erosion, and weathering patterns. It would therefore be valuable for future studies to assess how alternative reconstructions, such as those from V  rard (2019a) or Cerme  o et al. (2022), might influence these processes and the resulting oceanic response. Moreover, a simple nearest-neighbour scheme was used to route continental weathering products into the ocean; alternative watershed configurations could yield substantially different regional responses to astronomical forcing. Similarly, the use of HadCM3L, HadSM3, and GEOCLIM necessarily reflects one possible representation of climate and weathering dynamics; alternative emulator models or hydrological schemes could yield quantitatively different outcomes, although assessing the magnitude of such differences would require dedicated sensitivity experiments. The current setup also does not capture extreme events that may substantially influence sedimentary fluxes, and relies on a simplified organic matter sedimentation scheme that lacks O_2 dependence, highlighting the potential benefit of integrating more advanced models of organic matter diagenesis like OMEN-SED (H  lse et al., 2018) in future work. Additionally, the surface wind stress field is held constant throughout the simulations, preventing realistic changes in circulation patterns in response to evolving astronomical configurations. The exclusion of ice sheets and sea-level variations removes critical mechanisms through which obliquity can strongly impact $[\text{O}_2]$, although the accurate representation of sea-level changes would

3 | Spatially contrasted response of Devonian anoxia to astronomical forcing

remain challenging at the cGENIE grid resolution. Several studies have suggested that these processes may have contributed to, or exacerbated, Late Devonian OAEs (Bond and Wignall, 2008; Chen et al., 2013; Huygh et al., 2025). As a result, the influence of obliquity identified in this chapter may be underestimated, though it still leaves a discernible imprint on the global ocean. For all these reasons, we emphasize the importance of further modelling efforts to better connect orbital forcing with ocean anoxia. For instance, subsequent work would benefit from incorporating dynamic albedo and wind-stress profiles when exploring the full range of climate-circulation-biogeochemistry interactions. This is further encouraged by the results of Sarr et al. (2022), who showed that astronomically-driven changes in ocean circulation and ventilation can exert a strong control on oxygenation, with regional variations reaching up to $40 \mu\text{mol kg}^{-1}$ in a Late Cretaceous context. They could also explicitly test the robustness of the Late Devonian background state and its sensitivity to evolving external forcing across multiple models. In this context, EMICs offer a promising path forward, as they allow for long-timescale simulations while explicitly resolving many key physical and biogeochemical processes.

3.5 Conclusions

We have explored the role of astronomical forcing in driving ocean anoxia under a Late Devonian climate configuration. Our experimental setup relies on an offline coupling between cGENIE and a fast climate-weathering emulator, based on a GCM, developed by Sablon et al. (2025). It allowed us to capture the influence of astronomical forcing on oceanic $[\text{O}_2]$ via its modulation of continental PO_4 weathering fluxes. At the global scale, astronomical forcing exerts a moderate impact on ocean $[\text{O}_2]$, with the most pronounced deoxygenation occurring during intervals of combined high eccentricity and high obliquity. While eccentricity and precession primarily affect $[\text{O}_2]$ through their control on PO_4 weathering fluxes, obliquity exerts its influence by modulating the insolation component of biological productivity at high latitudes, highlighting that even in a greenhouse world, obliquity can leave an imprint on ocean biogeochemistry, hence possibly sedimentary records. At the regional scale, eccentricity maxima also correspond to the most extensive anoxic conditions,

providing new evidence supporting a strong impact of eccentricity maxima on the development of Late Devonian OAEs. However, the biogeochemical response remains highly variable across regions. Our results show that astronomical forcing can act as a dominant control on ocean $[O_2]$, driving regional changes in anoxic volume of up to 19 %. An unanticipated result is that local ocean circulation can represent a central driver of the spatial heterogeneity in $[O_2]$ responses to astronomical forcing. As a result, sedimentary records from different locations may reflect contrasting imprints of the same astronomical signal, potentially leading to contrasting interpretations of its role in pacing Late Devonian anoxia. Finally, while this chapter provides insights into how astronomical forcing affects Late Devonian ocean $[O_2]$, it also stresses the difficulty of explaining the duration of Devonian OAEs and the uncertainties in their spatial extent, underscoring that much modelling and data integration work remains to fully understand the drivers and dynamics of Late Devonian anoxia.

4

The Kellwasser Crisis: How to trigger global anoxia?

4.1 Introduction

In this chapter, we aim to quantify the perturbations that led to both Kellwasser events (at the F-F boundary) and to better constrain the spatial extent of anoxia during these events using data assimilation. This process involved an ensemble of simulations using cGENIE as well as compilations of measured geological redox indicators from the rock record to constrain the spatial distribution of anoxia (updated from Carmichael et al., 2019), combined with estimates of the seafloor anoxic fraction from Song et al. (2017a) and White et al. (2018), both based on uranium isotopes ($\delta^{238}\text{U}$). This approach allowed us to assess the large-scale spatial structure of ocean anoxia. The performance of each simulation was quantified using a scoring approach similar to that applied by Monteiro et al. (2012) for Late Cretaceous OAEs, with the seafloor anoxic fraction used as an additional constraint, to derive plausible perturbation scenarios. These scenarios provide order-of-magnitude estimates of the actual critical changes associated with the Kellwasser events and offer benchmarks against which proposed mechanisms for Late Devonian anoxia can be tested. This modelling method also underscores the importance of sampling both

4 | The Kellwasser Crisis: How to trigger global anoxia?

pre- and post-anoxic horizons in the field and assessing the baseline redox conditions of these pre- and post-anoxic horizons, so that models can more accurately reflect the perturbations responsible for marine anoxia.

4.2 Methods

4.2.1 Model description

The experiments use the default cGENIE configuration, as in Appendix A and Chapter 2, including the C-GOLDSTEIN framework and the BIOGEM and ATCHEM modules. Marine biogeochemistry is further coupled to the one-dimensional vertically resolved reaction–transport sediment model OMEN-SED (Hülse et al., 2018). This coupling avoids the need to impose a reflective boundary condition for POM, which would otherwise artificially enhance O_2 consumption at the seafloor (Hülse et al., 2021). The biological production follows a single-nutrient limitation scheme, based on PO_4 . All particulate PO_4 reaching the seafloor is instantaneously remineralized. Remineralization of exported organic matter in the water column is represented using an Arrhenius-type, temperature-dependent parameterization (Crichton et al., 2021). This parameterization increases remineralization rates in warmer waters and enhances nutrient recycling to the surface ocean, thereby supporting elevated biological production while preventing an artificially high extent of seafloor anoxia (Hülse et al., 2021). Both atmospheric pCO_2 and pO_2 are restored to fixed concentrations (with pO_2 set to modern values), thereby closing the global C and O_2 cycles. Fixing atmospheric $[O_2]$ to modern levels is consistent with recent estimates of F-F pO_2 ranges (Dahl et al., 2022; Mills et al., 2023; Sharoni and Halevy, 2023). The sinking rate of POM is reduced relative to standard modern configurations. This adjustment follows the common assumption that the smaller size of Late Devonian primary producers resulted in lower average sinking velocities (Lu et al., 2018). Following Heim et al. (2015), we estimate the mean biovolume of marine species to be $2.95 \log_{10} \text{ mm}^3$ for the Late Devonian, compared to $3.98 \log_{10} \text{ mm}^3$ today. Accordingly, the POM sinking rate is scaled from 125 m d^{-1} to 93.0 m d^{-1} ($2.95/3.98 \times 125$). Overall, the experimental design and key biogeochemical assumptions adopted here

follow those of Hülse et al. (2021). A full justification of these modelling choices and their implications can be found therein.

In all simulations used in this chapter, the ocean is represented on a 36×36 equal-area horizontal grid with 16 logarithmically spaced levels along the vertical (from 60 to 560 m). Palaeogeography is based on the reconstruction of Scotese and Wright (2018) for ~ 370 Ma and is implemented in cGENIE following the approach described in Chapter 3 (see Fig. 4.1). Minor adjustments are applied to ensure at least two vertical ocean grid cells per column and to reduce the depth of a specific grid cell, improving consistency between simulated $[\text{O}_2]$ distributions and geological constraints (see next section). The solar constant is set to 1325 W m^{-2} based on Gough (1981), the eccentricity to 0, as in Valdes et al. (2021), and the obliquity to $\sim 22.2^\circ$, which corresponds to the average value around the Kellwasser estimated by Laskar and Robutel (1993). Boundary conditions, including wind stress and surface albedo, are taken from Chapter 3 and ultimately derived from the HadCM3 simulation with 926 ppm pCO_2 presented in Valdes et al. (2021). Physical calibration of the coupled ocean–atmosphere system is taken from previous work by Cao et al. (2009) and Pohl et al. (2022).

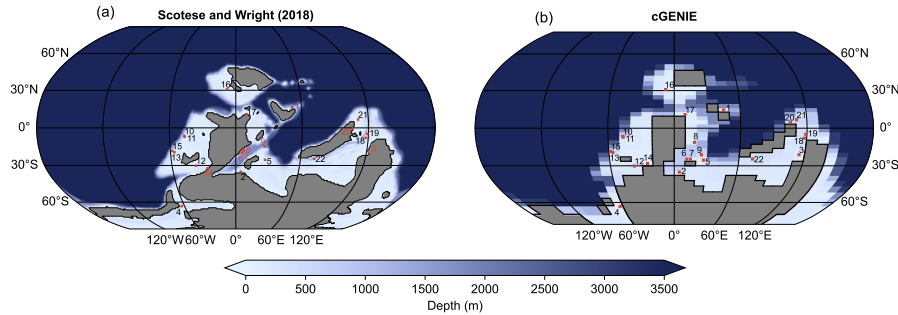


Fig. 4.1 *F-F bathymetry and data locations.* Devonian bathymetry (m) ~ 370 Ma based on (a) Scotese and Wright (2018) and (b) its representation at cGENIE resolution. Continents are shown in grey. Red squares indicate data locations, with numbers corresponding to Table 4.1. Numbers shown in red in panel (a) denote sites that were slightly adjusted to fall within the nearest shallow-marine settings of cGENIE.

4.2.2 Data description

We used an updated compilation of marine redox indicators presented by Carmichael et al. (2019) to constrain the spatial extent of ocean anoxia during

4 | The Kellwasser Crisis: How to trigger global anoxia?

the Kellwasser events (Table 4.1). This updated dataset integrates multiple independent lines of sedimentary and geochemical evidence to infer bottom water redox conditions and provides one of the most comprehensive syntheses currently available for both Kellwasser events. Locations were selected to ensure compatibility with the cGENIE framework, requiring that sites selected for the model clearly demonstrate the methodology for determining redox conditions. Sites that had redox data preceding or just after the events were included so that they could be clearly distinguished from redox conditions present during the Kellwasser intervals. The methods of determining redox conditions depend on a site's lithology (details in Carmichael et al., 2026, in review; Algeo and Liu, 2020), and therefore differ between sites and individual studies of each site (details provided in Appendix D.1, Table D.1).

#	Locations	O ₂ depletion state				References
		Pre-LKE	LKE	Pre- UKE	UKE	
1	West Junggar Basin (Boulongour Reservoir), Xinjiang, China	×	×	×	■?	Carmichael et al. (2014), Fan and Gong (2016), Shen et al. (2021), Shen et al. (2024), Shen et al. (2025), Song et al. (2017b), Stachacz et al. (2021), Suttner et al. (2014), Zhang et al. (2021), and Zheng et al. (2020)
2	Bou-Ounebdou - Gara de M'rirt, Azrou-Kenifra Basin, Morocco	×	●	×	●	Dopieralska et al. (2006), Joachimski et al. (2002), Lazreq (1992), Lazreq (1999), and Riquier et al. (2007)
3	McWhae Ridge, Lennard Shelf/Canning Basin, Australia			×	●	Becker et al. (1991), Goodfellow et al. (1988), Joachimski et al. (2002), McNamara and Feist (2016), and Playford et al. (1984)
4	Pando X-1 Core, Madre de Dios, Bolivia			▲	▲	Haddad et al. (2016)
5	Wolayer Glacier, Carnic Alps, Austria	×	●?			Bond et al. (2004), Buggisch and Joachimski (2006), Joachimski and Buggisch (1993), Joachimski et al. (1994), and Schönlaub et al. (2004)
6	Hony section, Namur-Dinant Basin, Belgium	×		×	●	Casier (2018), Claeys et al. (1996), Kaiho et al. (2013), Mottequin and Poty (2016), and Streel et al. (2000)
7	Benner Quarry, Rheinisches Schiefergebirge, Germany	×	▲	×	▲	Bond et al. (2004), Buggisch (1991), Buggisch and Joachimski (2006), Gereke and Schindler (2012), and Joachimski and Buggisch (1993)

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#	Locations	O ₂ depletion state				References
		Pre-LKE	LKE	Pre-UKE	UKE	
8	Kellwassertal, Harz mountains, Germany	×	■	×	■	Buggisch (1991), Gereke and Schindler (2012), Gereke et al. (2014), Joachimski et al. (1994), and Riquier et al. (2006)
9	Kowala Quarry, Holy Cross Mountains, Poland	×	■	×	▲	Bond et al. (2004), Chen et al. (2013), Joachimski et al. (2001), Joachimski et al. (2002), Kazmierczak et al. (2012), Narkiewicz and Hoffman (1989), Percival et al. (2019), Racki et al. (2002), Schwark and Empt (2006), and Stachacz et al. (2017)
10	Ancient Wall Section C (edge of Jasper Basin), Alberta, Canada	×	●	×	●	Whalen et al. (2015) and Whalen et al. (2017)
11	Miette Section W4 (edge of Jasper Basin), Alberta, Canada	×	●	×	●	Whalen et al. (2015) and Whalen et al. (2017)
12	IGS Sullivan Core, Illinois Basin, IA, USA	×	■	×	●	Day and Witzke (2017) and Uveges et al. (2018)
13	Devil's Gate, Great Basin (Woodruff and Pilot), NV and UT, USA	×	●	×	●	Bond and Wignall (2005), Morrow and Sandberg (2003), Sandberg et al. (1988), and White et al. (2018)
14	Walnut Creek section, Appalachian Basin, NY, USA	●	●	●	●	Boyer et al. (2014), Boyer et al. (2021), Chen et al. (2024), Cohen et al. (2022), Haddad et al. (2016), Haddad et al. (2018), Kelly et al. (2019), Lash (2017), Liu et al. (2022), Pippenger et al. (2023), Tuite Jr and Macko (2013), Uveges et al. (2018), and Zhao et al. (2022)
15	Whiterock Canyon section, Monitor Range, Nevada, USA	▲	▲	▲	▲	Bond and Wignall (2005) and Bratton et al. (1999)
16	Stolb Island, Lena River Delta, Siberia, Russia			●?	●	Yazikov et al. (2013) and Zhuravlev and Sokiran (2020)
17	Syv'yu River, Timan-Pechora Basin, Urals, Russia	×		●?	●	Gharaie et al. (2007), Racki et al. (2018), Yudina et al. (2002), and Zhuravlev and Sokiran (2020)
18	Mae Sarang section, northwestern Thailand			×	■	Dopieralska et al. (2012), Königshof et al. (2012), Racki et al. (2019), and Savage (2019)

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4 | The Kellwasser Crisis: How to trigger global anoxia?

#	Locations	O ₂ depletion state				References
		Pre-LKE	LKE	Pre-UKE	UKE	
19	Thong Pha Phum section, Satun Province, Thailand	×	×	×	×	Racki et al. (2019), Savage et al. (2006), and Savage (2019)
20	Yangdi (also referred to as Fuhe), Guangxi, China	×	■?	×	■?	Chen et al. (2005), Chen et al. (2013), Du et al. (2008), Gong et al. (2002), Gong et al. (2007), Huang and Gong (2016), Huang et al. (2018), Ma and Bai (2002), Ma et al. (2016), Ma et al. (2022), Wang et al. (2018), Wang et al. (2023), Whalen et al. (2015), Xu et al. (2008), Xu et al. (2012), Zeng et al. (2011), Zhang et al. (2017), and Zhao et al. (2024)
21	Xom Na section, Vietnam	×	■	×	■	Matsuo et al. (2020), Ta et al. (2022), and Thanh et al. (2013)
22	Howz-e-Dorah section, central Iran	×	●			Gharaie et al. (2004) and Gholamalian (2007)

Table 4.1 *Compilation of redox conditions. Geologically inferred local redox conditions before and during the LKE and UKE based on Carmichael et al. (2019). Evidence for oxygen-depleted conditions is represented by black dots (●, depletion severity unknown), squares (■, dysoxia), and triangles (▲, anoxia/euxinia), while evidence against is illustrated by crosses (×). Question marks (?) are used when evidence is limited.*

Application of these criteria yields a total of 22 data locations. At each site, redox conditions were assessed both before and during the Lower and Upper Kellwasser events, and the resulting classifications are summarized in Table 4.1. Present-day coordinates were reconstructed to their palaeogeographic positions at 370 Ma (see Fig. 4.1) using the pyGPlates software. At the spatial resolution of cGENIE, some reconstructed sites fall either on continental grid cells or at unrealistically large water depths, whereas Late Devonian redox records are derived predominantly from shallow-marine environments (Granot, 2016; Scotese and Wright, 2018; Carmichael et al., 2019). Small positional adjustments were therefore applied to ensure consistency with the model grid and bathymetry. All positional shifts are smaller than 10° in both latitude and longitude. For one site (data point 1), this criterion could not be satisfied; instead, the depth of the corresponding grid cell was artificially reduced (from ~1300 m to 300 m; see Fig. 4.1). However, all these adjustments remain small relative to the substantial uncertainties associated with Late Devonian palaeogeographic reconstructions (e.g., Fig. 2.1).

4.2.3 Experimental design

Our experimental design explores the combined effects of global mean $[\text{PO}_4]$ and atmospheric pCO_2 on ocean $[\text{O}_2]$. Global $[\text{PO}_4]$ is varied over a wide range, from 0.5 to 2.5 times preindustrial concentration ($2.159 \mu\text{mol kg}^{-1}$). This range is chosen following other studies on similar OAEs (Monteiro et al., 2012; Hülse et al., 2021) and because nutrient availability represents the principal perturbation investigated in this chapter. Atmospheric pCO_2 is varied independently across five levels: 1, 2, 4, 8, and 16 times preindustrial concentration (280 ppm), to account for the substantial uncertainty associated with Late Devonian pCO_2 levels. This selected pCO_2 range is informed by compilations of proxy- and model-based estimates for the Late Devonian, which suggest atmospheric $[\text{CO}_2]$ broadly spanning 500–3000 ppm (Smart et al., 2023). Nevertheless, values toward the lower end of this range are generally considered most likely (Chen et al., 2021; Dahl et al., 2022), meaning that the simulation using $16 \times$ preindustrial pCO_2 represents an extreme end-member scenario. All possible combinations of pCO_2 and $[\text{PO}_4]$ are explored, yielding a total of 45 simulations. Atmospheric pO_2 is held constant at preindustrial levels throughout all experiments, as it has been shown to be a reasonable approximation for Late Devonian conditions (Dahl et al., 2022). For clarity, preindustrial concentrations of pCO_2 , pO_2 , and $[\text{PO}_4]$ are hereafter referred to as $1 \times \text{pCO}_2$, $1 \times \text{pO}_2$ and $1 \times [\text{PO}_4]$, respectively. All simulations are integrated for 20 000 years to ensure that the system reaches equilibrium, and none exhibit limit cycles (i.e., oscillatory behaviour).

4.2.4 Scoring model-data comparison

Model performance is evaluated following the approach of Monteiro et al. (2012). For each simulation, a performance score Ψ is computed relative to the geological data using the formulation

$$\Psi = \left(\frac{\sum_i A_i W_i}{\sum_i W_i} + 1 \right) / 2, \quad (4.1)$$

where Ψ ranges from 0 to 1, with higher values indicating better agreement between model output and observations (e.g., a score of 0.4 implies agreement with 40 % of the data). Here, simulations with $\Psi \geq 0.7$ are considered to

4 | The Kellwasser Crisis: How to trigger global anoxia?

represent plausible states. This threshold corresponds to agreement with approximately two-thirds of the data and is considered appropriate given the uncertainties in palaeogeographic reconstructions, the limited spatial resolution of the model, and that geological constraints are almost exclusively derived from shallow-marine environments. The parameter W_i denotes the weight assigned to each data location and takes values of 0, 0.5, or 1, depending on the availability and robustness of redox information at a given site. In Table 4.1, the absence of a symbol corresponds to a weight of 0, a symbol with a question mark to 0.5, and a symbol without a question mark to 1. The agreement coefficient A_i quantifies the match between simulated and inferred redox conditions and varies between -1 (complete disagreement) and 1 (perfect agreement). Two distinct methods for computing the A_i coefficients were used in this chapter.

In the first method, the agreement metric exploits the full classification of redox states reported in Table 4.1. Maximum agreement ($A_i = 1$) is assigned when the model reproduces the inferred redox state, using $[\text{O}_2]$ thresholds after Sarr et al. (2022). Partial agreement is allowed when simulated $[\text{O}_2]$ fall outside the target redox interval but remain within $10 \mu\text{mol kg}^{-1}$ of its boundaries, with progressively lower values of A_i assigned as the mismatch increases. Two specific cases are treated as follows. For inferred anoxic conditions, partial agreement extends across the dysoxic range, reflecting that the model captures O_2 depletion even if the severity is underestimated. Conversely, when dysoxic conditions are inferred, and the model simulates anoxic conditions, a fixed positive agreement value is assigned (because of the limited width of the anoxic interval) to reflect the correct prediction of O_2 depletion.

Obviously, the computation of A_i substantially influences the resulting performance score. While the approach outlined above is designed to make consistent use of all available redox information, it explicitly relies on arbitrary choices. We therefore applied a second, more categorical computation of A_i . In this alternative approach, A_i is restricted to values of -1 or 1 and depends solely on whether the model predicts oxygen-depleted conditions (starting at the dysoxic threshold) at a given site. This binary computation, which drastically reduces the subjectivity of the A_i coefficient at the expense of redox-state detail, provides another way to evaluate model–data agreement. The two methods are reported in supplementary Fig. D.2 and supplementary Fig. D.3, respectively.

4.3 Comparing model simulation with geological records

The performance score Ψ was calculated for each simulation and is shown in Fig. 4.2. Higher scores indicate better agreement between simulated O_2 conditions and the spatial distribution of redox states summarized in Table 4.1 for each interval considered (pre-LKE, LKE, pre-UKE, and UKE). For both pre-event intervals, the maximum achievable score is 0.7, whereas a maximum score of 0.8 is obtained during both the LKE and UKE. The inability of the model to achieve higher scores reflects persistent mismatches at specific sites. During the pre-event intervals, sites 10 and 11 are consistently modelled as oxygen-depleted despite proxy evidence indicating oxic conditions. Conversely, reproducing the oxygen-depleted conditions inferred at site 14 requires at least $1.25 \times [PO_4]$, a forcing inconsistent with most other sites. In addition, sites 13 and 15 correspond to the same model grid cell but indicate contrasting redox states (oxic versus anoxic), a discrepancy that cannot be resolved at model resolution. During the LKE and UKE, site 19 remains oxic according to proxy evidence, whereas simulations predict oxygen depletion starting from $0.75 \times [PO_4]$ and onward. Furthermore, sites 2, 3, 6, and 7 require at least $2 \times [PO_4]$ and $4 \times pCO_2$ to reproduce inferred oxygen depletion, but these conditions simultaneously generate widespread anoxia, preventing agreement with sites characterized by dysoxia. Altogether, cGENIE successfully captures the first-order redox structure inferred from proxy records (Ψ of 0.7 and 0.8), but the systematic mismatches also reflect the model's limited ability to resolve local redox variability.

Identifying plausible simulations for the LKE and UKE requires additional constraints beyond spatial redox agreement alone (i.e., the performance score). Therefore, we used independent estimates of the seafloor anoxic fraction from Song et al. (2017a) and White et al. (2018), who inferred values reaching 7–9 % during the LKE and 18–20 % associated with the UKE, with pre-event seafloor anoxic fractions around 1–5 % (for both events). Simulated seafloor anoxic fractions for our ensemble are shown in Fig. 4.3, and the constraints from Song et al. (2017a) and White et al. (2018) are reported in Fig. 4.2 for the different time intervals. Additional constraints are also provided by estimates of Late Devonian atmospheric pCO_2 and temperatures, favouring simulations with 2 and $4 \times pCO_2$ (Lenton et al., 2018; Chen et al., 2021; Dahl et al., 2022; Wignall et al., 2026). Dahl et al. (2022) reported atmospheric pCO_2 of ~ 500 ppm

4 | The Kellwasser Crisis: How to trigger global anoxia?

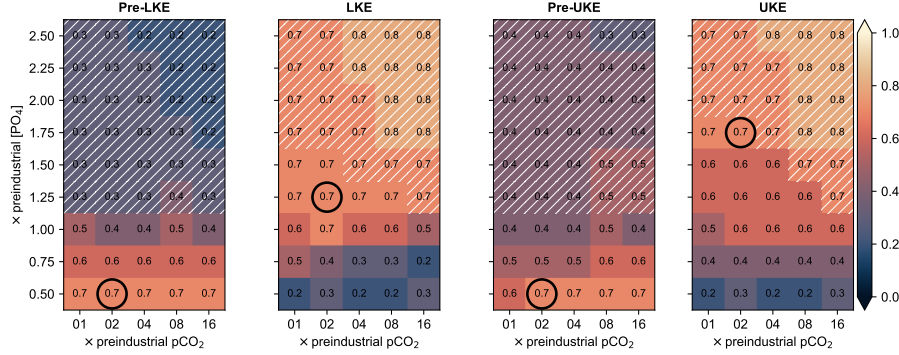


Fig. 4.2 Performance score (Ψ). Score computed for each simulation, using the method described in Section 4.2.4. A score of 0 means complete disagreement with the data from Table 4.1, while a score of 1 means complete agreement. Solid black circles highlight the simulation that best performed against all geological constraints (Ψ , seafloor anoxic fraction, and $p\text{CO}_2$ range). White hatched values represent simulations that are considered unrealistic compared to the estimates of the seafloor anoxic fraction from Song et al. (2017a) and White et al. (2018).

for the Devonian, associated with mean tropical surface air temperatures of roughly 24.5°C . In cGENIE, comparable tropical temperatures (26.5°C) are obtained with a $p\text{CO}_2$ of 560 ppm. In addition, recent estimates by Wignall et al. (2026) suggest a global mean temperature of about 22°C at the F-F boundary. The cGENIE simulations that show the closest agreement with this estimate are those with 2 and $4 \times p\text{CO}_2$, yielding global mean temperatures of 20.5 and 23.5°C , respectively. Applying these additional constraints excludes all simulations achieving the maximum performance score of 0.8, as these produce seafloor anoxic fractions far above geological estimates. Consequently, simulations with a performance score of 0.7 represent the only viable candidates for both events.

Within the explored parameter space, a global mean of $0.5 \times [\text{PO}_4]$ is the only configuration that yields satisfactory agreement with the geological data for pre-event conditions (i.e., a performance score ≥ 0.7 , see Section 4.2.4). A reduced global mean $[\text{PO}_4]$ is consistent with Sharoni and Halevy (2023), although $0.5 \times [\text{PO}_4]$ represents a lower-bound estimate of their range. With $0.5 \times [\text{PO}_4]$, the model performance for the pre-LKE interval is insensitive to $p\text{CO}_2$, whereas it only shows a weak dependence on $p\text{CO}_2$ for pre-UKE conditions. Acceptable agreement with the combined geological constraints is achieved at $1\text{--}1.25 \times [\text{PO}_4]$ for the LKE and $1.25\text{--}1.75 \times [\text{PO}_4]$ for the UKE.

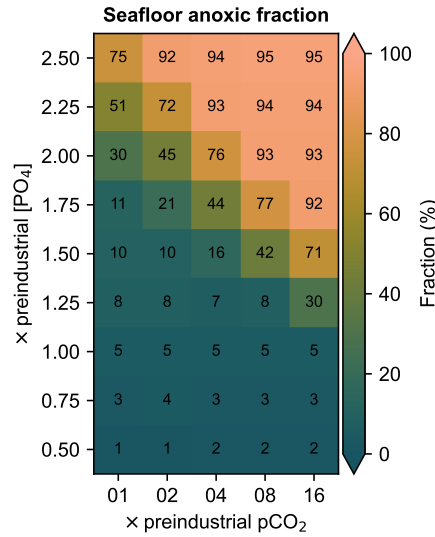


Fig. 4.3 Seafloor anoxic fraction. Seafloor anoxic fraction (in %) computed for each *cGENIE* simulation. These values are used to further constrain the simulations shown in Fig. 4.2.

These results imply that a perturbation, in the form of an increase of $0.5\text{--}0.75 \times [\text{PO}_4]$ relative to pre-event conditions, is sufficient to trigger the LKE, whereas a larger increase of $0.75\text{--}1.25 \times [\text{PO}_4]$ is required for the UKE. A larger perturbation for the UKE relative to the LKE could already be inferred from the estimates of seafloor anoxic fraction or the performance score computed in Fig. 4.2. However, considering both constraints together provides a more robust assessment, particularly as some Paleozoic intervals were characterized by a partial decoupling between the upper and deeper ocean (Pohl et al., 2021; Pohl et al., 2022).

These results show that an increase in nutrient availability alone can adequately reproduce the extent of anoxia during both Kellwasser events, whereas temperature changes alone are insufficient (see Fig. 4.2). This provides additional evidence that eutrophication is likely the main mechanism responsible for the widespread anoxic conditions observed during the Kellwasser event. The inferred nutrient increase needed to trigger the UKE is consistent with previous modelling studies, in which an increase of $1 \times [\text{PO}_4]$ was linked to major OAEs such as those of the Late Cretaceous and the Permian–Triassic (Monteiro et al., 2012; Hülse et al., 2021). Nevertheless, the smaller perturbation required for the LKE is notable, with plausible scenarios emerging from

4 | The Kellwasser Crisis: How to trigger global anoxia?

increases as low as $0.5 \times [\text{PO}_4]$, highlighting the non-uniform, time-specific level of perturbation needed to trigger an OAE.

The solid black circles in Fig. 4.2 identify the simulations that simultaneously achieve the highest performance scores while remaining consistent with independent constraints on seafloor anoxic fraction and atmospheric pCO_2 . These simulations are hereafter referred to as the best-estimate states for each of the four intervals considered. Although the LKE can be adequately simulated in the model with a nutrient increase of $0.5 \times [\text{PO}_4]$, improved agreement with the estimated seafloor anoxic fraction is obtained with an increase of $0.75 \times [\text{PO}_4]$. Similarly, while an increase of $0.75 \times [\text{PO}_4]$ is sufficient to initiate the UKE, the best agreement with geological constraints is achieved at $1.25 \times [\text{PO}_4]$.

Because the inferred perturbation magnitudes depend on the definition of the performance score, which involves some methodological choices, we repeated the analysis using a more categorical scoring approach. While showing differences from the first scoring method, results obtained using this binary scoring scheme are shown in supplementary Fig. D.2 and yield identical estimates of the required perturbations: $0.5\text{--}0.75 \times [\text{PO}_4]$ for the LKE and $1\text{--}1.25 \times [\text{PO}_4]$ for the UKE (see Appendix D.2).

4.4 Reconstruction of LKE and UKE

In their review, Carmichael et al. (2019) compiled a spatial synthesis of more than 150 studies investigating the Late Devonian Kellwasser events, providing a discrete representation of anoxic conditions while highlighting their strong spatial heterogeneity and inherent sampling biases. Building on this work, we reconstruct continuous global patterns of marine anoxia by identifying best-estimate states for the LKE and UKE (Section 4.3). Figures 4.4a and b show seafloor $[\text{O}_2]$ for the LKE and UKE, respectively. These simulations yield seafloor anoxic fractions of 8 % for the LKE and 21 % for the UKE (Fig. 4.3). During the LKE, anoxic conditions are largely confined to shallow-marine environments in the tropics, with no anoxia developing at seafloor depths greater than ~ 1000 m. Outside the 30°S – 30°N latitudinal band, much of the shallow ocean remains well-oxygenated, with $[\text{O}_2] > 62.5 \mu\text{mol kg}^{-1}$. In

contrast, the UKE is characterized by a much broader expansion of oxygen-depleted waters, extending to high southern latitudes and across large portions of the deep ocean seafloor. Dysoxic conditions even extend across most of the deep ocean seafloor, although these cannot be compared to existing geologic sample sets due to the subduction of these sediments. Nevertheless, a substantial fraction of shallow-marine environments remains well oxygenated, as during the LKE, although the extent of well-oxygenated shallow areas is reduced.

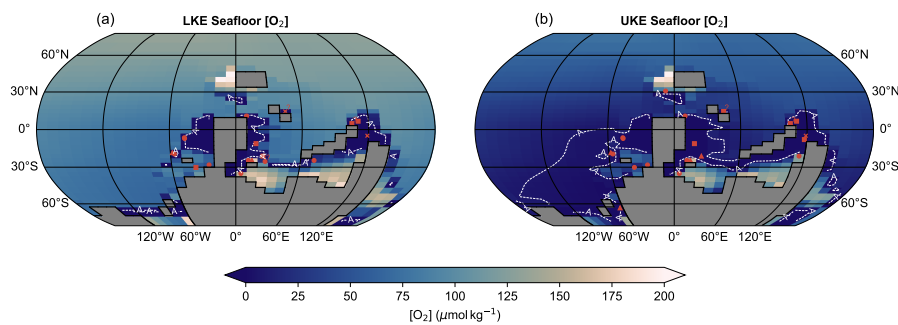


Fig. 4.4 Spatial extent of anoxic seafloor. $[O_2]$ at the seafloor for (a) the LKE and (b) UKE, estimated from Fig. 4.2. The LKE corresponds to the simulation with $1.25 \times [PO_4]$ and $2 \times pCO_2$, while the simulation for the UKE uses $1.75 \times [PO_4]$ and $2 \times pCO_2$. White dashed lines represent the anoxic region (A), with the threshold set at $6.5 \mu\text{mol kg}^{-1}$, after Sarr et al. (2022). As in Table 4.1, black dots (●, depletion severity unknown), squares (■, dysoxia), and triangles (▲, anoxia/euxinia) represent oxygen-depleted conditions, while crosses (×) illustrate oxic conditions. Question marks (?) are used when evidence is limited.

Overall, these results indicate that, although geological evidence for anoxia may appear globally distributed, vast regions of the shallow ocean likely remained well-oxygenated during both Kellwasser events. Accordingly, our simulations do not support scenarios in which shallow-marine environments became uniformly anoxic, even under extreme forcing (e.g., with $2.5 \times [PO_4]$ and $16 \times pCO_2$). The persistence of well-oxygenated regions also explains why performance scores do not exceed 0.7, as some data sites classified as anoxic fall within model grid cells that remain above O_2 depletion thresholds (as discussed in section 4.3). At a broader scale, the existence of these well-oxygenated shallow-marine settings suggests the presence of extra-tropical refuges for marine species during both events. Following the assumption that anoxia acts as the primary driver of the Kellwasser marine extinction, this implies that a globally uniform expansion of anoxia is not required to produce

4 | The Kellwasser Crisis: How to trigger global anoxia?

a major biodiversity crisis. Alternatively, it may indicate that anoxia alone does not fully account for the observed patterns of extinction, and that additional processes would have contributed. Resolving this question ultimately requires a better understanding of the response of Late Devonian marine ecosystems to widespread anoxic conditions and other environmental forcings.

For the LKE, the persistence of well-oxygenated deep waters argues against a “bottom-up” expansion of anoxia, pointing instead towards a “top-down” forcing. In this context, mechanisms such as astronomical forcing, volcanism, or the impact of terrestrial plant evolution on weathering are more likely to have triggered the LKE through enhanced nutrient delivery, rather than through changes in ocean circulation. In contrast, the widespread development of deep ocean anoxia during the UKE does not allow a clear distinction between these pathways.

However, the quantitative estimates derived here provide a useful framework to evaluate the plausibility of hypotheses and mechanisms. For instance, we showed in Chapter 3 that astronomically-driven variations in continental nutrient fluxes can generate regional increases up to $0.3 \times [\text{PO}_4]$. Compared to the larger perturbations inferred in this chapter, with best-estimates increases of $0.75 \times [\text{PO}_4]$ for the LKE and $1.25 \times [\text{PO}_4]$ for the UKE, this suggests that these astronomically-driven weathering fluxes contributed to these events but were insufficient, on their own, to account for their full magnitude. This interpretation is further supported by the spatially heterogeneous nature of the modelled $[\text{PO}_4]$ response to astronomical forcing reported in Chapter 3, which contrasts with the more widespread perturbations required to reproduce the extent of anoxia.

The overall consistency between simulated and observed patterns of anoxia supports that a single global perturbation can account for a large fraction of the available observations during the Kellwasser events. This reduces the need to invoke multiple diachronous episodes of localized anoxia mimicking a global signal, as proposed by Hedhli et al. (2023) for the Hangenberg crisis. Nevertheless, the modelling framework used here does not allow stronger conclusions regarding the synchronicity of Kellwasser anoxia and further emphasizes the need for improved spatial and temporal constraints. More generally, our results underscore the importance of extensive sampling in the pre- and post-anoxic intervals in order for models to run with sufficient baseline data.

5

Conclusions

5.1 Research results

OAEs represent some of the most profound disruptions of the marine environment in Earth's history and are closely associated with major ecological and biogeochemical changes. During the Devonian Period in particular, recurrent episodes of widespread ocean deoxygenation have been documented in the geological record, yet their underlying drivers remain highly debated. Numerous mechanisms have been proposed, but the relative importance of these processes, as well as their interactions, remains poorly constrained. To contribute to a better understanding of the Devonian OAEs, we relied on climate modelling using the EMIC cGENIE. Through a series of targeted numerical experiments, we explored the role of key environmental parameters in shaping ocean oxygenation. In doing so, we addressed the main questions outlined in the introduction of this thesis:

To what extent did the Devonian continental configuration influence OAEs?

Continental configuration exerts a first-order control on Devonian ocean oxygenation. This influence operates through both a direct effect on ocean cir-

culation and the establishment of palaeogeographic settings promoting anoxia, such as restricted basins. Even small variations in continental geometry can produce substantial consequences for ocean anoxia. Perhaps more importantly, continental configuration also influences anoxia indirectly by modulating the impact of other forcings, including temperature (through $p\text{CO}_2$), atmospheric $p\text{O}_2$, nutrient availability (PO_4), and astronomical forcing. This modulation effect can be strong enough to reverse effects on anoxia across different configurations. Altogether, these findings suggest that continental configuration may be the dominant control on OAEs, owing to the wide range of processes it influences. However, uncertainties in palaeogeographic reconstructions currently preclude a definitive quantitative assessment of its explicit role during the Devonian. Consequently, the main priority emerging from this work is the need for improved constraints on continental configurations. In the meantime, we encourage the systematic assessment of palaeogeographic uncertainty in deep-time modelling studies whenever feasible. While it remains challenging in practice due to computational costs, this approach also suffers from the limited availability of open-access continental reconstructions. Expanding open access to palaeogeographic reconstructions and associated tools would therefore greatly benefit the palaeoclimate community.

What is the quantitative impact of astronomical forcing on Devonian OAEs? Could it have paced anoxia?

The influence of astronomical forcing on Devonian OAEs, through its impact on continental nutrient fluxes, is highly spatially heterogeneous. Some regions exhibit a pronounced response, with variations in anoxic volume reaching up to 19 %, whereas others show only limited sensitivity. In addition, the dominant astronomical parameter, as well as the relative contribution of each parameter controlling $[\text{O}_2]$ variability, differ between regions. This heterogeneity helps explain why proxy records from different locations may record contrasting expressions of astronomical signals, leading to different interpretations of their role in driving ocean anoxia. Despite this variability, some consistent large-scale patterns emerge. In particular, our results provide further support for the eccentricity maxima hypothesis, with the most extensive anoxic conditions occurring under high eccentricity configurations and little to no evidence of long-term system memory as $[\text{O}_2]$ closely follows the precession signal. However, when compared with the magnitude of perturbations required to reproduce the Kellwasser events, the simulated variations in continental

nutrient fluxes appear insufficient to fully account for their extent. Overall, astronomical forcing emerges as an important driver of ocean oxygenation variability through its control on nutrient fluxes, but is unlikely to act as a standalone pacing mechanism for the major Devonian OAEs within the framework explored here. This result should not be interpreted as a rejection of astronomical forcing as a potential trigger of Devonian anoxia, but rather as motivation to consider additional processes, including glacio- and limno-eustasy, vegetation feedbacks, changes in wind stress, and albedo variations, in future modelling frameworks. Only by capturing the full range of these mechanisms will it be possible to robustly assess whether astronomical forcing acts as the primary pacer of Devonian OAEs or not.

How global was the first-order Kellwasser event, and what magnitude of environmental perturbation would be required to trigger such an OAE?

By integrating spatial constraints on anoxia with independent estimates of seafloor anoxic fraction, we identified a restricted set of simulations that successfully reproduce both Kellwasser events and quantitative constraints on the magnitude of their associated environmental perturbations. The results indicate that eutrophication alone is sufficient to reproduce the observed extent of anoxia, supporting nutrient enrichment as a primary driver. Perhaps more importantly, the main contribution of this work lies in establishing quantitative benchmarks against which competing mechanisms can be evaluated. In particular, these benchmarks proved central to the conclusions of the previous question: the nutrient flux variations driven by astronomical forcing, while contributing to background modulation, fell short of the threshold required to reproduce the full extent of the Kellwasser events. More generally, the multiplication of such independent benchmarks appears to offer a promising path toward increasingly constrained and quantitatively robust reconstructions of Devonian OAEs. This approach allows proposed mechanisms to be evaluated not only qualitatively, but also in terms of their ability to reproduce physically consistent environmental states.

5.2 Perspective

In the end, the use of cGENIE, and more broadly of EMIC and climate modelling, has proven to be a valuable approach for exploring Devonian OAEs. However, it is essential to acknowledge the substantial uncertainties that still surround these events. These uncertainties affect nearly all aspects of Devonian OAEs, from their timing and duration to the exact sequence of processes leading to their onset. Although some of these uncertainties were explicitly explored in this thesis, all results ultimately rely on a single modelling framework, however well suited it may be. A natural next step would therefore be to assess the robustness of these findings using other climate models, which could provide complementary or contrasting perspectives on Devonian OAEs.

This thesis only scratches the surface of the processes governing OAEs, and countless questions remain open. In particular, the duration of these events remains poorly constrained and relatively unexplored from a modelling perspective. While several mechanisms have been proposed to explain anoxic persistence, a comprehensive framework allowing their quantitative evaluation is still lacking. In this context, reduced-complexity approaches, including EMICs and conceptual models, offer a promising avenue to investigate OAEs dynamics. Adopting this dynamical systems perspective may help clarify how features such as hysteresis, multistability, and oscillations influence ocean oxygenation and contribute to the persistence of anoxic conditions. Notably, although Chapter 2 considered hysteresis as a possible explanation for long timescales, it did not uncover a clear physical mechanism behind these extended durations, suggesting the potential for further investigation. More broadly, it remains unclear how the relative importance of the mechanisms influencing OAEs and their interactions may have evolved under the changing boundary conditions of the Phanerozoic. Addressing such questions requires moving beyond isolated case studies toward a more integrated and systematic use of climate modelling. A key challenge will also be to better define how ocean anoxia is represented and diagnosed in models, and to clarify how different metrics of anoxia, such as seafloor anoxic fraction, OMZ extent, average $[O_2]$, and anoxic water volume, relate to one another.

More fundamentally, it appears highly unlikely that a clear consensus on the precise triggers of Devonian OAEs will be reached in the near future.

Even for well-observed components of the modern climate system, such as the AMOC, important debate persists regarding whether it has actually weakened over the last decades or not (Rahmstorf et al., 2015; Terhaar et al., 2025). In comparison, reaching a precise consensus on events that occurred ~ 370 Ma, based on incomplete and indirect geological evidence, appears like a nearly impossible challenge. This suggests that achieving full consensus on such deep-time events is currently out of reach. Accordingly, the objective should perhaps not be the identification of a single definitive mechanism, but rather to evaluate the relative plausibility of different scenarios. In this context, focusing on common features shared by multiple hypotheses, rather than on competing interpretations, may provide a productive way forward.

Within this broader perspective, the role of continental configuration emerges as central, as many mechanisms proposed for OAEs depend directly on palaeogeographic boundary conditions. Initiatives such as “DeepMIP-Phan” represent a promising direction for future research. Such efforts enable a more systematic assessment of how uncertainties in palaeogeography influence climate and ocean dynamics across different modelling frameworks. They will also help identify robust features, or “invariants”, of the climate system that persist across models and palaeogeographic reconstructions. For instance, certain large-scale ocean circulation patterns or their responses to external forcing may prove to be relatively insensitive to paleogeographic uncertainties and model differences. Conversely, if no such invariants can be identified, this would demonstrate that robust geological constraints on palaeogeography are mandatory for producing any realistic reconstruction of deep-time climates.

Throughout this thesis, a broad shift occurs in the perspective regarding the study of climate systems, moving from a predominantly physical climate–dynamical framework, as exemplified in Appendix A, toward a more biogeochemistry-oriented approach. Hence, important opportunities remain for a more physically based understanding of climate dynamics, particularly related to the strong uncertainties associated with boundary conditions such as continental configuration. Questions about the structure of ocean circulation in such different configurations remain only partially understood. For instance, how can the pressure gradients required for deep-water formation develop in a continental-free hemisphere with flat bathymetry? While not always directly linked to the question of anoxia, these physical oceanographic challenges are highly relevant for improving our understanding of past climate systems, which continue to exhibit many unresolved dynamics.

5 | Conclusions

The plurality and diversity of perspectives highlight how much remains to be understood when it comes to ocean anoxic events. Personally, I find this particularly exciting, as it opens the door to extensive exploratory work in the years and decades ahead. The journey continues!



Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

A.1 Introduction

A commonly used illustration for the global oceanic circulation is that of a conveyor belt driven by both wind stress and buoyancy fluxes at the ocean-atmosphere interface (Dijkstra, 2005). This chapter focuses on the thermohaline part of this circulation and, more specifically, on the AMOC. The AMOC emerges as the result of three contributions, which are (1) the preconditioning of salty water mass and its horizontal northward advection, (2) the buoyancy loss due to exchanges with the atmosphere, and (3) the density gradient across the water column resulting from convection. This convection occurs primarily at subpolar latitudes in the Labrador and Greenland seas and maintains the large-scale circulation via the geostrophic balance between the pressure and Coriolis forces (Weijer et al., 2019). It is widely known (e.g., Dijkstra, 2005) that the atmospheric buoyancy fluxes have opposite contributions to the AMOC; a purely thermal circulation would have a downwelling flow in the north that follows the sinking of colder water in the North Atlantic, with

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

upper and deep flows propagating towards the northern polar and equatorial regions, respectively. On the contrary, a strictly haline circulation would have a downwelling flow located in the equatorial zone due to the sinking of saltier water at the Equator, with upper and deep flows propagating towards the equatorial and northern polar regions, respectively. The current balance has water masses sinking to depths of 2–3 km, forming the North Atlantic Deep Water (NADW), which propagates southward until it reaches the surface again (Rhein et al., 2017). About 80 % of the ocean deep water returns to the surface in the Southern Ocean, while the remaining portion returns to the sea surface via upwelling to the thermocline at low latitudes (Tamsitt et al., 2017). It is now well established that the AMOC is a crucial part of the climate system due to its essential contribution to the global circulation, which itself acts as a redistribution system that transports large amounts of heat and salt throughout the Northern Hemisphere (Jungclauss et al., 2006). Even if the current AMOC slowdown remains an open question, models predict a substantial AMOC slowdown if atmospheric $[\text{CO}_2]$ continues to increase (Caesar et al., 2021; Kilbourne et al., 2022; Latif et al., 2022; Zhu et al., 2023). A reduction in the AMOC would cause an equatorward shift in the Intertropical Convergence Zone (ITCZ), a weakening of the Asian and Indian summer monsoons, and a cooling of the Arctic (Buckley and Marshall, 2016).

The potential triggers and mechanisms for changes, possibly abrupt, in the AMOC and the associated impacts on the climate system are still an active area of research (Mehling et al., 2022). Specifically, the possibility that the THC could exhibit bistability and hysteresis (quasi-irreversibility) was suggested more than 60 years ago (Stommel, 1961; Rahmstorf, 1996). Bistability has since been identified and studied across a wide range of models, though not all models exhibit this feature with the present boundary conditions (Rahmstorf et al., 2005; Hawkins et al., 2011; Weijer et al., 2019; Jackson et al., 2023). For the AMOC, the different states would correspond to vigorous versus weak overturning and are often referred to as on vs. off states, respectively (Jackson et al., 2017). It is not excluded that, with global warming, the AMOC will end up being locked in an off state, but a more likely scenario is that the AMOC will undergo a transient decay and partial recovery (Jackson et al., 2023; Weijer et al., 2019).

As a general rule, anomalies in temperature and freshwater input, particularly close to the convection zone, can decrease ocean density and weaken the circulation. Then, different feedbacks are crucial in determining how and

when the circulation may be brought to a potential collapse. On the one hand, this weakening decreases heat transport to the north, thereby increasing ocean density in a negative feedback loop. On the other hand, the decrease in salt transport amplifies the initial perturbation in a positive feedback loop called the advective salinity feedback. The response of the atmosphere may further interact with these feedbacks by modulating heat and freshwater exchanges. However, as the ocean salinity does not feedback directly on precipitation, salinity anomalies are able to propagate freely and are decisive in amplifying the perturbation via the advection feedback (Dijkstra, 2005).

To explore the circulation response and the related mechanisms, authors usually choose to force the system either with freshwater fluxes or atmospheric $[\text{CO}_2]$. What value these forcings need to reach to induce a complete shut-down of the circulation depends on the model (Liu et al., 2017) and on their rate of increase (Stocker and Schmittner, 1997). In many models, when the atmospheric $[\text{CO}_2]$ increases from preindustrial levels, it causes a weakening or even a collapse of the AMOC mainly through the reduction in the vertical density gradient (Thorpe et al., 2001). To investigate some mechanisms of the slowdown, Hirschi and Marotzke (2007) developed a diagnostic based on the thermal wind relationship. Specifically, they reconstruct the overturning streamfunction using the thermal wind balance. Then, fixing either the temperature or the salinity field to the initial conditions of a transient experiment allows us to examine the haline and thermal contributions to the variations in the overturning streamfunction. Levang and Schmitt (2020) applied this diagnostic to analyse the output of 26 models of the CMIP5 experiment in response to the Representative Concentration Pathway 8.5 (RCP8.5) scenario. Overall, they concluded that temperature dynamics are responsible for AMOC weakening, while freshwater forcing instead acts to strengthen the circulation.

The objective of this chapter is twofold. First, we apply the same diagnostic as Levang and Schmitt (2020) to the cGENIE framework, which contains the efficient C-GOLDSTEIN climate model (Marsh et al., 2011). Because this model is used in many palaeo and future climate studies, we want to know where this model stands with respect to the CMIP5 standard models. In this respect, this chapter is a contribution towards the documentation of a model widely used in palaeoclimate research. For example, it was used to explore past ocean acidification by illustrating the variation in ocean CO_3 properties under different atmospheric CO_2 perturbations (Hönisch et al., 2012), reconstruct the carbon cycle dynamics during the Palaeocene–Eocene thermal maximum

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

event (Gutjahr et al., 2017), and investigate the Pacific meridional overturning circulation during the last glacial maximum (Rae et al., 2020). Second, due to its lower complexity level, cGENIE allows us to do long experiments at a relatively small cost. It implies that we will be able to examine, with the Levang and Schmitt (2020) diagnostic, how the thermal and haline contributions unfold until several centuries/millennia after the collapse, when the ocean salinity and temperature fields have reached equilibrium. Then, by comparing the output of the experiments with CO₂ and freshwater forcing, we may critically examine what this diagnostic approach tells us about the nature of the forcing.

A.2 Methods

A.2.1 Model description

In our experiments, we used the default configuration of cGENIE, which includes the C-GOLDSTEIN framework together with the BIOGEM and ATCHEM modules, while all other modules were disabled. The ocean is represented on a 36×36 horizontal equal-area grid, with 16 logarithmically spaced levels along the vertical (from 80 to 765 m). The equal-area feature of the horizontal grid results from the uniform spacing in the longitude and the sine of the latitude. The continental configuration and the boundary conditions are the ones used in Crichton et al. (2021), which correspond to a preindustrial climate (atmospheric [CO₂] of 280 ppm), while all the ocean and atmosphere parameters are taken from Cao et al. (2009). We use the originally prescribed moisture transport from the Atlantic to the Pacific (as the AMOC is not able to sustain without it in cGENIE) and modify atmospheric diffusivity over the Southern Ocean and Antarctica, as well as the sea ice diffusivity parameter – as in Ödalen et al. (2020) and Crichton et al. (2021) – to improve the seasonal sea ice properties in the Southern Ocean. The seasonal cycle of solar radiation is activated, as well as the climate response to changes in atmospheric CO₂. To obtain a configuration corresponding to a preindustrial climate equilibrium, an extended simulation of 30 000 years is conducted using an atmospheric [CO₂] of 280 ppm. This state provides the initial condition for both sets of experiments (RCP8.5 and hysteresis) presented below.

A.2.2 Geostrophic approximation

Since the AMOC is nearly geostrophically balanced at the interannual timescale, the transport can be determined using thermal wind and density profiles obtained from the zonal boundaries of the basin, as reported in Buckley and Marshall (2016). The diagnostic presented in Levang and Schmitt (2020) uses this thermal wind balance to build a geostrophic streamfunction to approximate the one computed by the CMIP5 models. In their study, they showed that for all the models considered, this approximation is good, especially when it comes to estimating the maximum of the streamfunction. To compute the geostrophic streamfunction, we first need the expression of the meridional velocity v_g as a function of depth. It is obtained from the thermal wind balance as follows:

$$v_g(z) = \frac{g}{\rho_0 f} \int_{-H}^z \frac{1}{L(z)} (\rho_w - \rho_e) dz, \quad (\text{A.1})$$

with z , the depth variable, verifying $-H \leq z \leq 0$; g is the gravitational acceleration; ρ_0 is the reference density; f is the Coriolis parameter; H is used as the ocean depth; $L(z)$ is the basin width; and ρ_w and ρ_e are the density on the western and eastern margins, respectively. The density fields used for the computation of the meridional velocity are either directly used from the model output (if available) or generated offline from the temperature and salinity fields, using the state equation of density. In cGENIE, this state equation is a third-order polynomial approximation of the UNESCO equation of state (Winton and Sarachik, 1993). The expression of the geostrophic streamfunction is then obtained by integration of the meridional velocity

$$\Psi_{\text{geo}}(z) = \int_{x_w}^{x_e} \int_{-H}^z \left(v_g(z) - \frac{1}{H} \int_{-H}^0 v_g(z) dz \right) dz dx, \quad (\text{A.2})$$

where mass conservation is achieved by removing the depth average velocity. This allows the streamfunction to fulfil the condition $\Psi_{\text{geo}}(z) = 0$ for $z = 0, -H$. In the north, the Atlantic basin is open through the Bering Strait, implying water exchanges on the order of about 1 Sv. These exchanges are not included in our approximation because they are relatively small compared to the total overturning. The full development of the thermal wind diagnostic and

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

the related geostrophic streamfunction can be found in Hirschi and Marotzke (2007).

A.3 Results

A.3.1 RCP8.5

Thermal wind diagnostic

cGENIE is forced with the atmospheric $[\text{CO}_2]$ of the RCP8.5 scenario used in the CMIP5 ensemble. Our RCP8.5 simulation runs from a preindustrial climate to the year 3000, with results presented only from the year 2000 onward. This set-up allows for realistic behaviour and direct comparison with the work of Levang and Schmitt (2020).

Figure A.1a shows the overturning streamfunction associated with the AMOC in Sverdrups ($1 \text{ Sv} \equiv 10^6 \text{ m}^3 \text{ s}^{-1}$) for the year 2000. The streamfunction in cGENIE is weaker than in the multimodel mean and hardly reaches a maximum of 13 Sv compared to 20 Sv for the CMIP5 multimodel mean. While the difference is significant, it is not a strong cause for concern, as climate models show great variability in the reconstruction of the overturning strength. The CMIP5 models also have maximum AMOC values ranging from 10 to 30 Sv around the year 2000, with cGENIE falling into that range. As already mentioned, the geostrophic approximation proves to be a reliable method for estimating the streamfunction maximum, which is located a bit south of 54° N (specifically at 53.66° N) in cGENIE. Figure A.1b illustrates the spatial pattern of the AMOC following 1000 years of the RCP8.5 scenario, while Fig. A.1c shows the time series of different streamfunction maximums at a latitude of 54° N . The AMOC will have completely collapsed by the year 3000, with Antarctic waters having filled most of the Atlantic basin. The collapsed character of the AMOC can be further confirmed by inspecting the $[\text{O}_2]$ profile of the Atlantic, known as a reliable proxy for water ages (not shown here) (Marshall and Plumb, 2008).

The collapse of the AMOC under the RCP8.5 scenario in cGENIE did not surprise us. In our preparatory work, we observed that the AMOC collapses

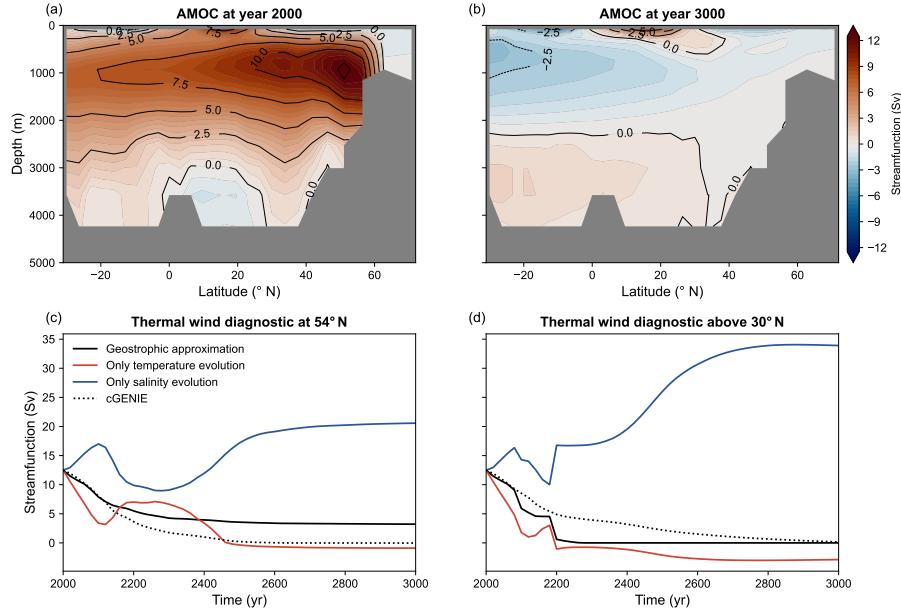


Fig. A.1 AMOC weakening in cGENIE. Measure of the AMOC strength (Sv) using the cGENIE streamfunction as a function of latitude and depth under the RCP8.5 warming scenario, corresponding to the years (a) 2000 and (b) 3000. Bold flow lines are spaced by 2.5 Sv. Time series of the overturning maximum (c) at 54° N and (d) considering all latitudes above 30° N, starting from the year 2000. The solid and dotted black curves represent the maximum of the streamfunction computed with the geostrophic approximation and cGENIE, respectively. The red and blue curves represent the maximum of the geostrophic streamfunction when only the temperature (red) or salinity (blue) evolution is considered. Here, the separate temperature and salinity contributions do not exactly sum to equal the total geostrophic approximation because the maxima of their respective streamfunction often appear at close but different depths (see Fig. A.5d–f).

between $[\text{CO}_2]$ of 5 and $6 \times \text{PAL}$ when $[\text{CO}_2]$ slowly increases (specifically, 5000 years to move from n to $n + 1 \times \text{PAL}$). However, we also found that a collapse of the AMOC occurs for lower $[\text{CO}_2]$ if the increase rate is higher, as is the case in this experiment. Rate-dependent tipping of the AMOC is a well-established phenomenon, as already described by Stocker and Schmittner (1997), that has been shown and analysed more recently in a global ocean model (Lohmann and Ditlevsen, 2021). The RCP8.5 scenario happens to trigger this rate-induced tipping.

To investigate the respective contributions of temperature and salinity, two partial geostrophic streamfunctions are derived offline from density fields. Similar to Levang and Schmitt (2020), these fields are generated using the

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

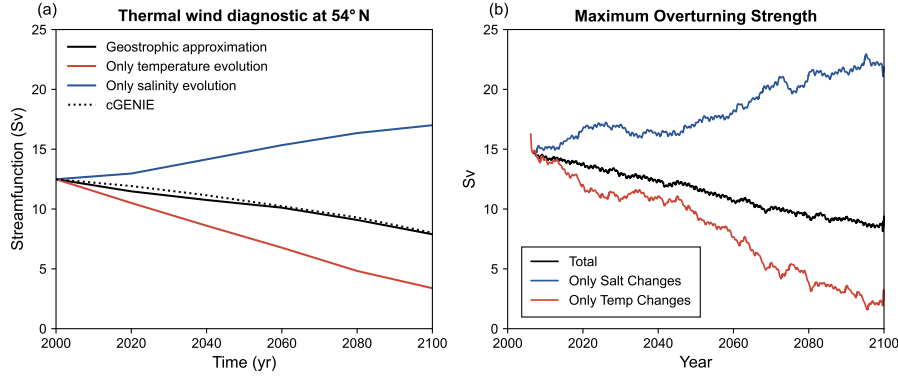


Fig. A.2 *Performance of cGENIE against the CMIP5 multimodel mean. Comparison of the diagnostic obtained with cGENIE (a) and the multimodel mean made by Levang and Schmitt (2020) (© American Meteorological Society. Used with permission.) (b), visible in the top-left panel of their Fig. 4, where the colours are adapted to match our conventions.*

temperature or salinity evolution only, keeping the other variable equal to its initial distribution. We find that throughout the experiment, temperature and salinity fields alternate their respective contributions to the geostrophic streamfunction anomaly. Specifically, three distinct phases emerge, taking place between 2000–2100, 2100–2300, and 2300–3000 years, respectively (Fig. A.1c). The phases are bounded by changes in the concavity of the two partial geostrophic streamfunctions (the blue and red curves in Fig. A.1c). The geostrophic streamfunction decreases throughout the simulation, and this evolution results from partially compensating contributions of temperature and salinity, which tend to act against each other.

During the first 100 years of the simulation (phase 1), the cGENIE and geostrophic streamfunctions (respectively, the dotted and solid black curves in Fig. A.1c) are very close to each other, attesting to the adequacy of the geostrophic approximation. This is not surprising, considering that C-GOLDSTEIN, the ocean circulation model, uses a friction-geostrophic approximation to estimate the circulation. Furthermore, the behaviour of the diagnostic obtained is very similar to the multimodel mean made by Levang and Schmitt (2020) (see Fig. A.2). If we follow Levang and Schmitt (2020), the results suggest that the thermal component of the circulation induces a significant weakening, while the haline component acts to strengthen the streamfunction, with the net effect being a decrease in the AMOC strength. However, we also observe that

during the next 200 years (phase 2), the respective contributions of temperature and salinity to the overturning circulation reverse their trends. The thermal forcing acts to increase the geostrophic streamfunction, and the haline forcing causes a decrease. For the remaining part of the simulation (phase 3), the trend reverses again, with the temperature and salinity fields regaining their initial contribution, as seen for the first 100 years of the experiment. These trend inversions have not been observed by Levang and Schmitt (2020), possibly because the corresponding CMIP5 experiments were too short to evidence it.

Driving mechanisms

We now provide a more in-depth analysis of the behaviour of the geostrophic function components. In Eq. A.2, the overturning streamfunction is a vertical integral of the geostrophic velocity – following the principle of the thermal wind balance – down to the ocean sea floor. The geostrophic velocity at depth z is, in turn, the vertical integral of the zonal density gradient. Consequently, the zonally integrated geostrophic streamfunction depends on the values of density on the western and eastern sides only. In the initial condition, the thermal contribution is positive and dominates that of the salinity, which is negative, justifying the statement that the streamfunction is mainly thermally driven (see Fig. A.3).

During the first phase of the simulation (year 2000 to 2100), the increase in surface temperature reduces the intensity of deep-sea mixing at convection sites in the northeastern Atlantic. On the western side of the ocean, the temperature increases along most of the water column because the heat is no longer effectively evacuated by the convection process. On the eastern side, where convection does not normally occur in this model, the combined action of the atmospheric forcing (positive) and the reduced vertical ventilation in the west causes only moderate warming. Thus, the western margin experiences a greater warming trend than the eastern one, leading to a reduction in the zonal density gradient across nearly the entire water column, which in turn weakens the streamfunction (see Fig. A.4a). The warming of the western margin has previously been identified as the leading cause of AMOC weakening (Levang and Schmitt, 2020). This effect is partly compensated for by a reduction in the east–west salinity gradient, which, as we recall, tends to act against the overturning streamfunction (see Fig. A.3b and d). Indeed, the equatorial advection of salt propagates less extensively towards the east, depriving the

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

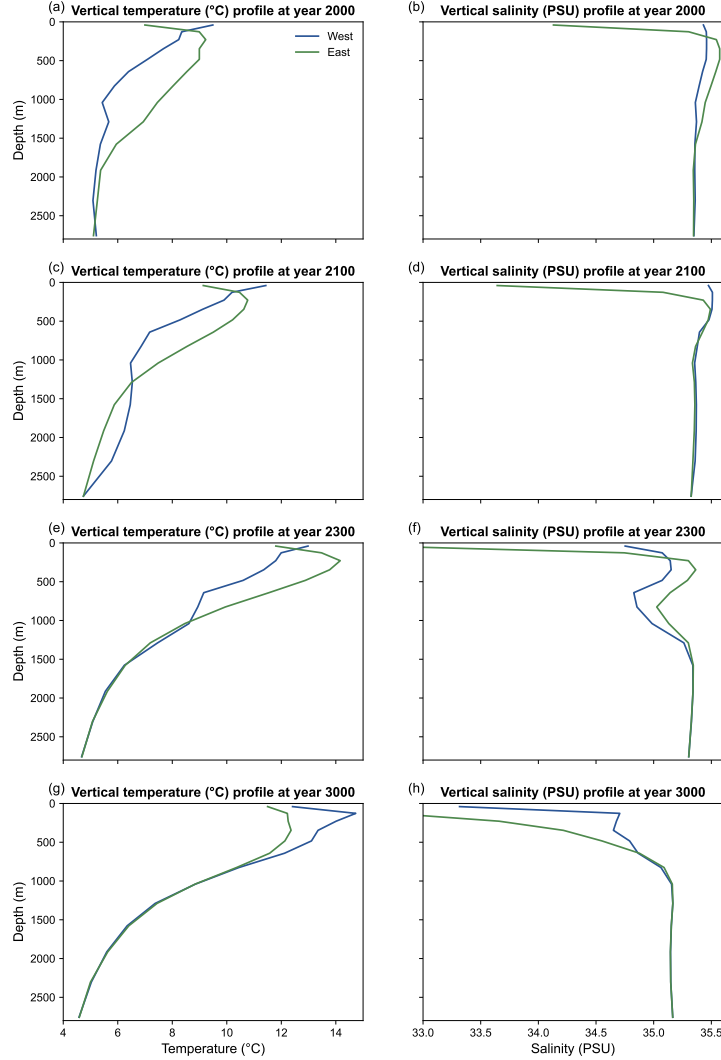


Fig. A.3 Vertical temperature and salinity profiles. Temperature (left) and salinity (right) values along the western (blue) and eastern (green) Atlantic margin at 54° N.

eastern boundary of a source of salt while leaving the west almost unchanged. This causes a reduction in the density along the first 1500 m of the eastern basin margin, thereby reinforcing the geostrophic overturning (see Fig. A.4d). Again, because density variations induced by temperature perturbations are larger than those resulting from salinity, the overall modification of density induces a weakening of the streamfunction, justifying the driving role played by temperature during this phase (see Fig. A.5a and d).

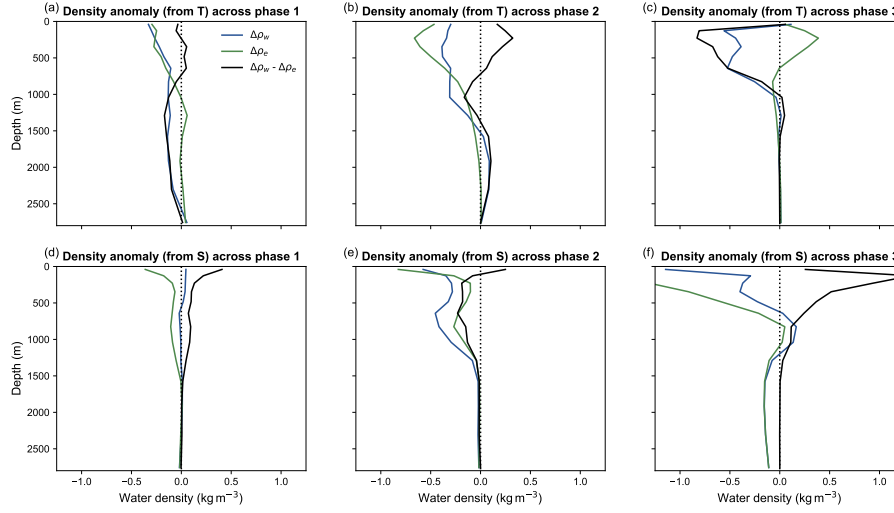


Fig. A.4 Vertical density anomaly profiles. Values along the eastern and western Atlantic margins at 54° N for each of the three phases (2000-2100, 2100-2300 and 2300-3000). These anomalies arise either from temperature T (a-c) or salinity S changes (d-f). The blue and green curves represent the density anomaly at the eastern and western margins, respectively, that arises during a phase (difference between the end and the beginning of a phase). The solid black curve shows the total zonal density anomaly. The dotted black curve separates the positive from the negative density anomalies.

As the intensity of the overturning decreases, less buoyant water is being advected from the equatorial regions to the north via the western boundary current. This prepares the second phase (year 2100 to 2300), which is marked by a reduction and southward shift in the overturning cell, depriving the first 1500 m of the western boundary of a source of warm and salty water. On average, the western boundary experiences lower warming compared to the east, but it loses more salinity (see Fig. A.4b and e), and this further reduces the zonal density gradient (and doing so the streamfunction). Below 1500 m, the thermal and haline fields homogenise due to the decrease in the depth of the AMOC. The salinity gradient at depth is fairly close to what it was during the first phase of the experiment. However, as the western boundary is no longer supplied with warm water, its temperature decreases compared to the year 2100; it cools, and this is now the temperature that partially compensates for the salinity effect that drives the slowdown of the AMOC (see Fig. A.5b and e).

During the final phase (year 2300 to 3000), the driving mechanism shifts towards the mixing and contamination of lower ocean layers by Antarctic

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

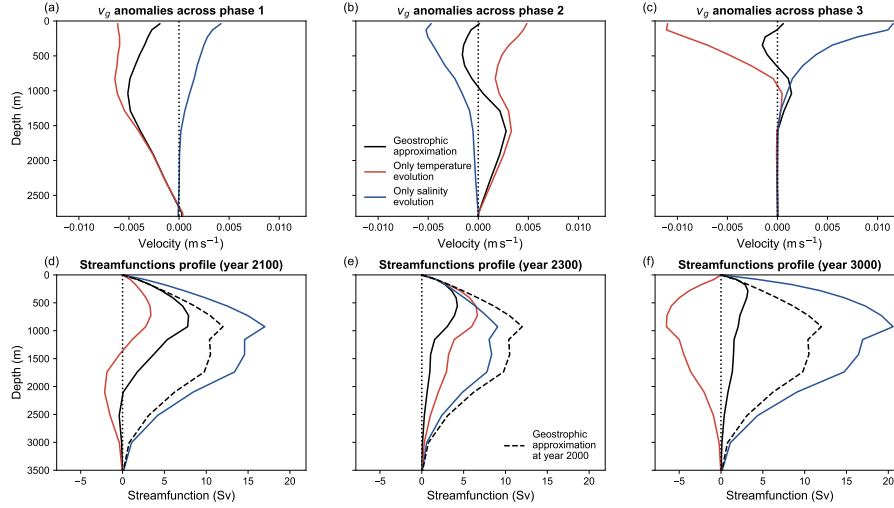


Fig. A.5 Vertical geostrophic velocity and streamfunction profiles. Vertical profiles of geostrophic velocity anomalies at 54° N for each of the three phases (a) 2000-2100, (b) 2100-2300 and (c) 2300-3000. Vertical profiles of different streamfunctions at 54° N for the year (d) 2100, (e) 2300 and (f) 3000. The solid black curve represents the portrayed quantity computed with the geostrophic approximation. The red and blue curves represent the same quantity when only the temperature (red) or salinity (blue) evolution is considered. The dashed black curve (d-f) represents the streamfunction computed with the geostrophic approximation of the initial condition (year 2000). This figure represents the relationship between the zonal density gradient (see Figure A.4) and the streamfunction maximum illustrated in Figure A.1c.

waters, which follows the complete shutdown of deep convection. Although deep circulation stops, the subtropical gyre continues to operate and allows relatively warm and saline waters to propagate northward along the western boundary (see Fig. A.4c and f). These inputs cause the first 750 m (mainly through eddy diffusion) of the western boundary to be warmer and saltier than on the eastern boundary, maintaining the horizontal density differences at these depths. This explains why the geostrophic streamfunction in Fig. A.1c never properly reaches 0 but rather converges to a value around 3 Sv. For the rest of the water column, the contamination of Antarctic Bottom Water and mixing completely homogenise the thermal and haline fields, making their contribution to the zonal density gradient negligible. As a result, during this final phase, temperature changes drive, again, the weakening of the streamfunction, with the remaining zonal density gradient being only maintained by the surface circulation (see Fig. A.5c and f).

We also observe that the quality of the geographic approximation deteriorates around year 150, when compared to the initial condition, although it stays decent for the entire run. We attribute this deterioration to the latitude shift in the streamfunction maximum when the AMOC weakens. Because the CO_2 increase forces the overturning cell to move southward, one could apply the thermal wind diagnostic while staying at the latitude of the streamfunction maximum (see Fig. A.1d). This method seems more relevant, but tracking the maximum of the overturning streamfunction implies changing the latitude of the diagnostic as the overturning cell moves. Due to the coarse spatial resolution of cGENIE, each of the abrupt jumps in the geostrophic curves corresponds to a change in the latitude of the streamfunction maximum. We found, however, that south of 30°N , as the Coriolis factor is smaller and the thermal wind approximation becomes more questionable, the difference between the true value and the geostrophic approximation could reach about 10 Sv. Whether using the geostrophic diagnostic at a fixed latitude of 54°N or tracking the latitude as the overturning streamfunction shifts, does not qualitatively affect the results discussed so far (curves shown in Fig. A.1d are very similar to those shown in Fig. A.1c). One clearly distinguishes the same three phases along the decrease in the maximum overturning streamfunction. This sensitivity analysis of the diagnostics confirms that the three phases that we have identified are not an artefact of using a fixed latitude (54°N) but rather a more widespread feature throughout the North Atlantic. However, one has to note that the timing and demarcation of these three phases can differ from one latitude to another.

A.3.2 The nature of the forcing

Having established the underlying mechanisms that lead to the weakening of the AMOC in cGENIE, our next goal is to investigate the information that can be inferred about the nature of the forcing applied to the circulation using the same diagnostic. To reach this goal, two different hysteresis experiments are conducted, with one using CO_2 and the other freshwater. Simulations involve a linear increase and subsequent decrease (symmetric in time) of the forcing value over a period of 40 000 and 20 000 years, respectively (see Fig. 6). In the CO_2 experiment, the $[\text{CO}_2]$ is incrementally increased from 1 to $10 \times$ the preindustrial concentration in 18 000 years after staying constant for 2000 years. Simulations show that, in cGENIE, the system has to stay at low

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

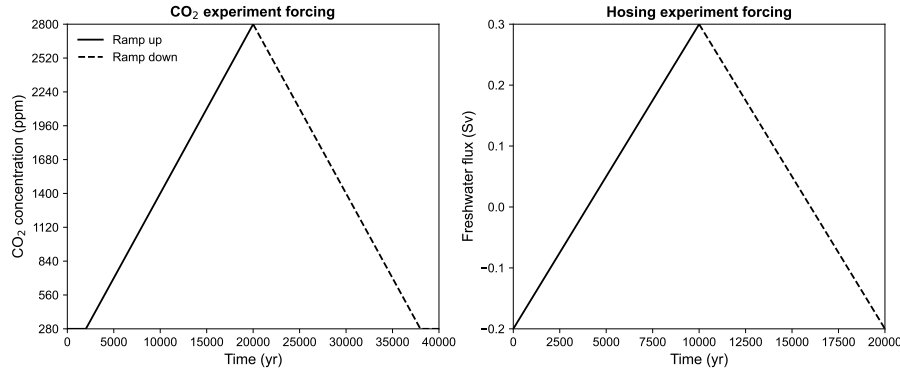


Fig. A.6 Time evolution of CO_2 and freshwater forcings. Schematic of atmospheric CO_2 (a) and freshwater (b) forcing for the hysteresis experiments. Solid and dashed lines represent the transient increase and decrease in the forcing, respectively.

atmospheric $[\text{CO}_2]$ for several hundreds of years to allow the circulation to recover. The freshwater hosing experiment is identical to the one realised in Rahmstorf et al. (2005). It involves the addition of freshwater in a uniform manner to the latitude band of $20\text{--}50^\circ\text{N}$ across the Atlantic with a rate of change of $0.05\text{ Sv per }1000\text{ model years}$. Targeting these latitudes is driven by the motivation to avoid direct forcing of the high-latitude convection regions. With this framework, the model is forced from -0.2 to 0.3 Sv in $10\,000$ years. The slow variation in the forcing rates keeps the system in a quasi-equilibrium state, which is crucial for hysteresis experiments.

Figure A.7a and b show the results for experiments of hysteresis forced by atmospheric $[\text{CO}_2]$ and freshwater flux, respectively. Figure A.7a includes two curves, namely a solid one representing the maximum streamfunction at 54°N and a dotted one showing the same maximum but considering all latitudes above 30°N . As for the RCP8.5, only the curve at a fixed latitude will be studied, as it differs very little from the second one, except for a more abrupt recovery of the AMOC and a slight underestimation of the streamfunction value when it is low. The second curve is used as further verification of the robustness of the diagnostic already tested in Section A.3.1. Figure A.7b also includes two curves, where the solid one corresponds to the maximum streamfunction at 54°N with a total ocean salt inventory kept constant, and the dotted one represents the same curve but with an open salt inventory. To achieve a constant salinity inventory in the experiment, the freshwater forcing applied across the Atlantic is compensated for by applying the exact opposite forcing but distributed over

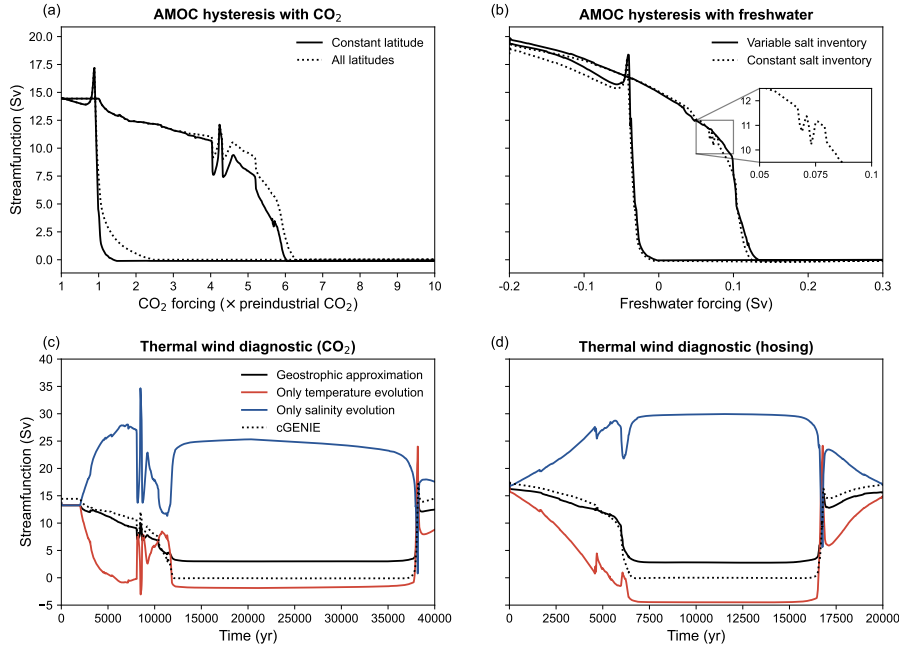


Fig. A.7 Hysteresis experiments and thermal wind diagnostic. Hysteresis curves of the cGENIE streamfunction maximum obtained with a (a) CO_2 and (b) freshwater forcing. In panel (a), the two black curves represent the overturning maximum at 54°N (solid), and consider all latitudes above 30°N (dotted). (b) For the freshwater forcing, two different simulations were conducted, namely one with a constant salinity inventory (dotted black line) and another where the inventory is left variable (solid black line). Panels (a) and (b) exclusively feature two hysteresis simulations each (one dotted and one solid). Each simulation is then composed of two different parts; there is one where the forcing increases, and there is another where it decreases. The thermal wind diagnostic was performed for the (c) CO_2 and (d) freshwater with variable salt inventory hysteresis experiments. The evolution in panels (c) and (d) is expressed in years, with the corresponding forcing being indicated in Fig. A.6.

the Pacific. Overall, the two curves show close similarities, providing evidence that the open/close aspect of the total ocean salt inventory is not of major importance in this experiment. While this result has already been previously observed in the original study (Rahmstorf et al., 2005), it serves as a verification of our experimental design and the robustness of our findings.

Figure A.7c and d represent the thermal wind diagnostic of the hysteresis experiment with CO_2 and freshwater, respectively. They show the time evolution of the same quantities, as in Fig. A.1c, at a latitude of 54°N . As previously mentioned, the geostrophic approximation allows proper reconstruction of

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

the streamfunction in cGENIE. Similarly, the hysteresis experiment with CO_2 exhibits the presence of the three phases identified in the RCP8.5 experiment (see Fig. A.7c). The first phase (from 1 to $3 \times \text{PAL}$) is where the streamfunction slowdown is driven by changes in thermal structure and is mainly due to the weakening of the convection. The second phase (from 3 to $5.5 \times \text{PAL}$) is characterised by an equatorward shift in the overturning cell, which generates a predominance of the salinity signal in the weakening of the overturning circulation as the northward advection of warm and salty waters diminishes. The final phase (from 5.5 to $10 \times \text{PAL}$) is governed by the mixing and contamination of Antarctic Bottom Water, which reverses the trend one last time, with a complete stoppage of the AMOC that is maintained by the thermal field. At the end of the simulation, an overshoot is observed. The overshoot at AMOC recovery is often observed in models (Rahmstorf et al., 2005) and is a transient effect related to the accumulation of buoyancy in the off state of the circulation. Here, we find that this phenomenon is mainly thermally driven, with the salinity gradient working against the temperature gradient. The fact that this hysteresis experiment with CO_2 displays close similarities to the RCP8.5 is not very surprising, except for the presence of a sawtooth-shaped event around $4 \times \text{PAL}$ that we will explore later on.

Perhaps more surprising is that the hysteresis experiment with the freshwater flux has a similar ratio between thermal and haline contributions to that of the RCP8.5 (see Fig. A.7d) because we know that, in the former case, the forcing is freshwater and not temperature. We are not the first to find that freshwater hosing is able to reduce the strength of the AMOC through temperature effects, as similar findings have already been achieved by Haskins et al. (2020). Again, we see three phases (the second one is slightly shorter), with the trends dominated overall by the changes in the thermal structure of the ocean, and with salinity taking the lead for the actual shutdown of the circulation. Having a similar decomposition and behaviour of the temperature and salinity changes in experiments with two clearly different forcings (CO_2 in Fig. A.7a and freshwater in Fig. A.7c) comes as a warning that the thermal wind diagnostic is indicative of the inner structure and response of the AMOC, but it does not inform us about the nature of the forcing applied to it. Therefore, only using this offline diagnostic does not allow separating the respective contributions of temperature and freshwater flux changes on the weakening of the AMOC that comes with the increase in the atmospheric $[\text{CO}_2]$.

Now we return to the sawtooth-shaped event visible on both curves of Fig. A.7a. We find that this sawtooth behaviour is a furtive occurrence of an oscillation that is triggered as the system evolves in quasi-equilibrium under particular $[\text{CO}_2]$. The oscillation regime is also triggered in the freshwater-forcing hysteresis experiment, but the oscillation is weaker and only appears when the freshwater flux forcing in the Atlantic is compensated for in the Pacific (see magnified view in Fig. A.7b). The occurrence of natural oscillations in the AMOC on the multicentennial/millennial timescale is a familiar phenomenon that has been observed across many different models (Sakai and Peltier, 1997; Thornalley et al., 2009; Peltier and Vettoretti, 2014; Sévellec and Fedorov, 2014; Li and Yang, 2022; Vettoretti et al., 2022). In cGENIE, some millennial oscillations have been highlighted by Keane et al. (2025) for different ranges of atmospheric $[\text{CO}_2]$ and an idealised continental configuration. Oscillations in the THC have also been observed in cGENIE as freshwater forcing is applied to the system when close to a bifurcation point (Lenton et al., 2009). Self-sustained oscillations in the ocean can have different origins, and a full investigation of the mechanism of their specific occurrence here is beyond the scope of this chapter. However, these oscillations are responsible for the outstanding excursions in the diagnostic of thermal wind observed around year 8000 in Fig. A.7c, yet they do not alter the three distinct phases identified.

A.4 Discussion and conclusions

This study builds on the work of Levang and Schmitt (2020), who used the thermal wind diagnostic and various general circulation models to examine the AMOC weakening under the RCP8.5 warming scenario. Here, we used cGENIE first to get some further confidence about the representation and sensitivity of the AMOC in this model, widely used for palaeoclimate studies, and also because we wanted to better understand the value of the diagnostic itself. We established close similarities with the CMIP5 models during the corresponding time interval of the RCP8.5 scenario. We also highlighted the three-phase structure of the circulation collapse scenario with, first, the weakening of the convective mixing driving the thermal zonal gradient over the first 1500 m of the water column across the North Atlantic; then the northward advective weakening via the western boundary current drives a decrease in the salinity

A | Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale

gradient; and, finally, the collapse and invasion of much of the Atlantic by Antarctic-origin waters, with a surface density gradient persisting mainly through the surface gyre circulation. The three-phase structure is robust across different experimental set-ups, whether the primary driver is CO₂ increase or freshwater forcing. We found that the interplay between temperature and salinity is crucial for the shutdown of the circulation, with the initial slowdown being thermally driven and the salinity taking the lead for the termination of the overturning. We also tested the robustness of the implementation details of the diagnostic. Specifically, tracking the latitude of the maximum of the overturning streamfunction or staying localised at 54° N generates the same conclusions.

These results invite us to suggest a caveat, with respect to Levang and Schmitt (2020), following our conclusions:

Therefore, in CMIP5, temperature dynamics are responsible for AMOC weakening, while freshwater forcing instead acts to strengthen the circulation in the net. These results indicate that past modelling studies of AMOC weakening, which rely on freshwater hosing in the subpolar gyre, may not be directly applicable to a more complex warming scenario.

In this chapter, we showed that the thermal wind diagnostic does not allow us to conclude whether variations in the AMOC produced under an increase in CO₂ are mainly driven by freshwater or heat flux exchanges with the atmosphere. In our simulations, even a pure freshwater forcing induces a slowdown of the AMOC driven by the temperature field, and similar results were also found by Haskins et al. (2020) when using two distinct general climate models. This lack of information is a consequence of running simulations where neither the temperature nor the salinity field is kept constant, meaning that the temperature field is influenced by circulation modifications induced by changes in the salinity field, and vice versa. As a result, the signal of the perturbation forcing becomes increasingly weaker over the course of the simulation before disappearing completely from the offline thermal wind diagnostic. On the other hand, we agree with Levang and Schmitt (2020) on the relevance of using [CO₂] to constrain the AMOC. While the large majority of studies showcase the hysteresis behaviour of the AMOC using only a freshwater input, we manage to show that it can also be obtained by considering a CO₂ forcing. Interestingly, the hysteresis curve forced by CO₂ has revealed features that were less obvious with the hosing experiment,

highlighting the potential benefits of considering different approaches when forcing the AMOC.

The present findings contribute to the overall discussion about the suitability of EMICs, such as cGENIE, to study the response of the large-scale THC. In the past, the cGENIE framework has proven to be a relevant choice for analysing large-scale THC (Rahmstorf et al., 2005; Lunt et al., 2006; Lenton et al., 2007; Cao et al., 2009; Marsh et al., 2013; Keane et al., 2025). These findings also provide additional evidence that cGENIE can exhibit natural stable oscillations on the millennial timescales for a modern continental configuration, whether the system is forced with CO₂ or freshwater.

However, there are some well-known limitations associated with the model that need to be taken into consideration, such as its coarse spatial resolution, a simplistic representation of the continents and the associated hydrological scheme, the absence of ice sheets, and the lack of a dynamic atmosphere. Specifically, the atmospheric feedback in cGENIE is fairly elementary, with precipitation not responding as it would in a full general circulation model. For example, wind stress does not respond to climate change, and yet, this response could have different impacts on the gyre circulation and on the deep-water mixing in both the Southern and the Northern hemispheres. Furthermore, the coarse spatial resolution can induce an inadequate representation of circulation dynamics, particularly at high latitudes. The simplistic hydrological scheme and the absence of ice sheets lead to flaws in freshwater fluxes along coastal margins, which can in turn influence the overturning.

Despite all these drawbacks, the model is able to reproduce the general trend of the multimodel mean used by Levang and Schmitt (2020), and the simplifications that are made allow for long-term simulations with a much more reasonable computation time. In this context, the similarity between the diagnostic scenario of the first phase of the collapse scenario in cGENIE and that found in CMIP class models (Levang and Schmitt, 2020) has proved to be fairly reassuring. We are in a position to suggest that the three-phase development of the AMOC collapse that we have found here could also occur in CMIP class models. To our knowledge, this has not been tested so far, and we would naturally encourage such an investigation to document similarities and potential differences between this EMIC and finer models.

B

Appendix to Chapter 2

B.1 Limit cycle in Scot420M

Our goal is to explore the unusual shape of the limit cycle observed in the Scot420M continental setup. Similar to Scot390M, we find that these oscillations arise from the interplay between advective and convective feedbacks. However, differences between the two oscillations suggest that another mechanism is at play for Scot420M (see Fig. 2.9a and b). In this configuration, the observed oscillations emerge as a composite of a similar limit cycle as in Scot390M and a deep-decoupling oscillation. This additional deep decoupling oscillation involves the gradual accumulation of heat below the surface, as shown in Fig. B.1. Mack (2021) have also observed analogous deep decoupling oscillations, manifesting as two quasi-stable states – an unventilated phase and a ventilated phase – using the MITgcm ocean model for Devonian palaeoclimate conditions. Furthermore, the close similarity between Fig. A1 and Fig. 3.8 from Mack (2021) further demonstrates the ability of cGENIE to capture complex large-scale ocean dynamics patterns. The combination of these two limit cycles generates this “two-step” pattern of the oscillations present for the Scot420M continental configuration (see Fig. 2.9a and b).

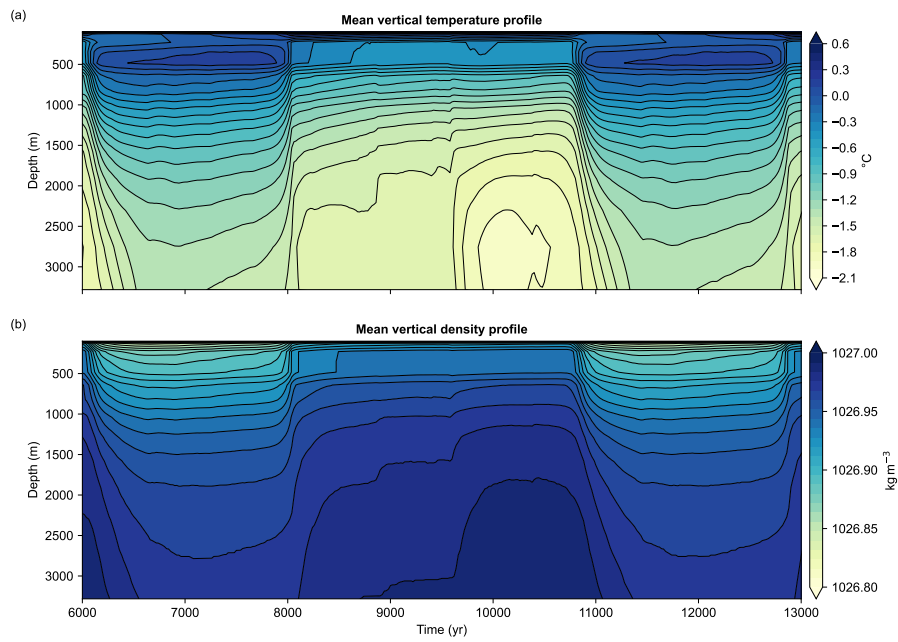


Fig. B.1 *Oscillations using Scot420M continental configuration. Representation of the mean vertical (a) temperature and (b) density profile for Scot420M. The simulation has been performed using $2 \times p\text{CO}_2$, $1.75 \times [\text{PO}_4]$ and $0.7 \times p\text{O}_2$.*

C

Appendix to Chapter 3

C.1 Background state and ocean circulation

Figure C.1a, b, and d show a strong hemispheric asymmetry in oxygenation, with a substantially more oxygenated Northern Hemisphere compared to the Southern Hemisphere. This pattern primarily reflects large-scale ocean circulation (Fig. C.1e), which allows well-oxygenated surface waters to ventilate the deep ocean in the Northern Hemisphere. In contrast, a pronounced OMZ develops across much of the Southern Hemisphere (Fig. C.1d), where meridional overturning circulation is nearly absent. The OMZ is shallower towards low latitudes, where primary productivity is high, consistent with enhanced biological oxygen demand (Fig. C.1c). Primary productivity is also relatively elevated at high latitudes, while minimum values occur at mid latitudes, where downwelling associated with subtropical gyres prevents primary productivity. The seafloor $[O_2]$ map further indicates that most anoxic conditions at the seafloor are restricted to shallow ocean regions, as confirmed by comparison with the model bathymetry (Fig. 3.2c). These shallow regions therefore correspond to areas where sedimentary P regeneration feedbacks are expected to be strongest.

Changes in ocean circulation associated with astronomical forcing are small in our simulations, with a maximum variation in overturning strength

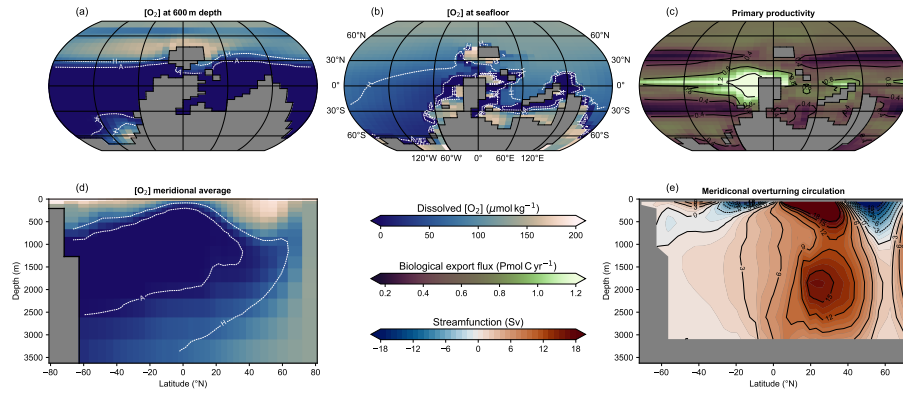


Fig. C.1 *Background state at the end of SPIN3. $[O_2]$ at a depth of 600 m (a) and at the seafloor (b). (c) Primary productivity ($Pmol\ C\ yr^{-1}$). (d) Meridional average of $[O_2]$. (e) Meridional overturning streamfunction ($1\ Sv \equiv 10^6\ m^3\ s^{-1}$). The white dashed lines in (a), (b), and (d) indicate the boundaries for the anoxic (A) and hypoxic (H) regions, with threshold values taken after Sarr et al. (2022).*

of 0.7 Sv (Sverdrup) when all orbital parameters vary together (0.56 Sv for eccentricity–precession forcing and 0.32 Sv for obliquity alone). Figure C.2 further indicates that the main regions of deep-water formation remain largely unchanged between extreme orbital configurations (extracted from the 1.1 Myr transient simulation). This small variability likely reflects the absence of dynamical changes in ocean circulation associated with orbital variations across the simulations. It may also indicate that the large-scale ocean circulation in cGENIE is not sufficiently sensitive to variations in surface albedo and wind stress forcing. Overall, the spatial distribution of deep-water formation explains the global overturning circulation pattern shown in Fig. C.1e.

C.2 Defining regions

This section clarifies how we refined the definition of the different regions based on the temporal variance of $[O_2]$ and $[PO_4]$. Figure C.3 shows the normalized temporal variance of these two tracers, averaged over the upper 1000 m, consistent with the depth range applied in our regional analysis (see Section 3.2). First, a clear distinction between regions SA and WL emerges from both $[O_2]$ and $[PO_4]$ variance fields, particularly around $30^\circ\ S$ and $60^\circ\ W$, providing strong justification for separating them. Second, region LG was initially split into

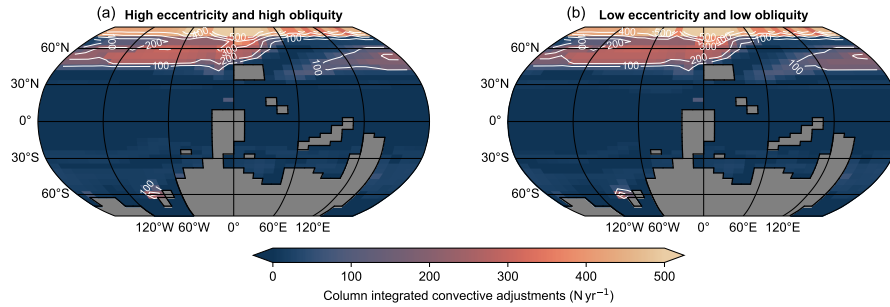


Fig. C.2 Deep water formation. Convective adjustments (expressed as the number of convective adjustments integrated across the water column per year) for (a) high eccentricity-high obliquity and (b) low eccentricity-low obliquity astronomical configurations.

two sub-regions based on the spatial structure of the variance fields. However, the temporal evolution and variability of $[\text{O}_2]$, anoxic volume, and $[\text{PO}_4]$ were found to be highly consistent across these sub-regions. Consequently, we merged them into a single, unified region, which we now refer to as region LG. These refinements provide a clear and consistent basis for the regional definitions presented in Fig. 3.4a. Although regional boundaries are somewhat arbitrary, they follow coherent patterns of variability and are broad enough to avoid overinterpreting hyper-localised phenomena (at the single grid cell level). The resulting regions are not intended as universal classifications, but rather as a practical framework for exploring the spatial heterogeneity of climate–biogeochemical interactions.

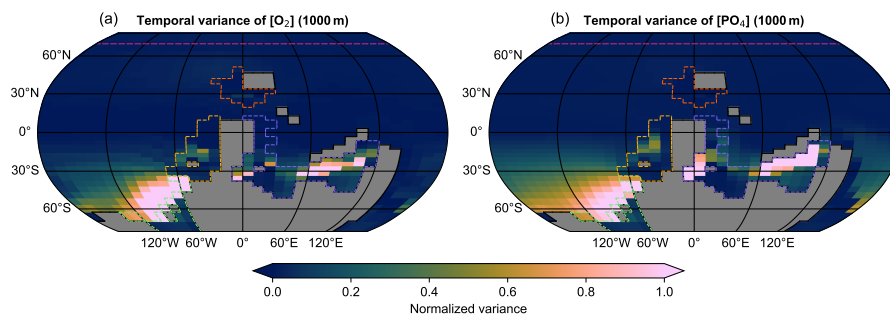


Fig. C.3 Temporal variance. Normalized temporal variance of (a) $[\text{O}_2]$ and (b) $[\text{PO}_4]$ averaged over the upper 1000 m. Dashed coloured lines indicate regional boundaries, as defined in Fig. 3.4.

D

Appendix to Chapter 4

D.1 Data locations: redox evidence and lithology

#	Locations	LKE		UKE	
		Evidence	Lithology	Evidence	Lithology
1	Central Asian Orogenic Belt: northwest China	None, sediments do not support tracers	Volcaniclastic cobbles	Trace elements and possible framboidal pyrite	Limestone and silt, volcaniclastic cobbles
2	Gondwana: Africa - Morocco	Bituminous limestone	Bituminous limestone	Black shales	Black shales
3	Gondwana: Australia	LKE not observed	LKE not observed	Trace elements	Limestones
4	Gondwana: South America - Bolivia	LKE not discussed	LKE not discussed	Organic biomarkers	Black shales
5	Laurussia - Europe: Austria	None or black shales according to Buggisch and Joachimski (2006)	Limestone or black shales according to Buggisch and Joachimski (2006)	UKE not observed	UKE not observed

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D | Appendix to Chapter 3

#	Locations	LKE		UKE	
		Evidence	Lithology	Evidence	Lithology
6	Laurussia - Europe: Belgium	LKE not noted	LKE not noted	Black laminated shales	Black shales
7	Laurussia - Europe: Germany	Pyrite framboids, ichnofabrics	Black lime-stones/shales	Pyrite framboids, ichnofabrics	Black lime-stones/shales
8	Laurussia - Europe: Germany	Pyrite framboids, trace elements	Black marlstones and limestones	Pyrite framboids, trace elements	Black marlstones and limestones
9	Laurussia - Europe: Poland	Trace elements and pyrite framboids	Limestones and marl	Trace elements and pyrite framboids	Limestone and marl
10	Laurussia - North America: Canada	Trace elements	Limestones	Trace elements	Limestones
11	Laurussia - North America: Canada	Trace elements	Limestones	Trace elements	Limestones
12	Laurussia - North America: Iowa, USA	Lacking evidences	Highly condensed, calcareous mudstone	Black shales	Black shales
13	Laurussia - North America: Nevada, USA	Pyrite framboids, U isotopes and rock geochemistry	Calcareous mudstone, limestone con-glomerates and bituminous deposits	Pyrite framboids, U isotopes and rock geochemistry	Siltstone, shales, bituminous deposits
14	Laurussia - North America: New York, USA	Geochemistry and ichnofabrics	Black shales	Geochemistry and ichnofabrics	Black shales
15	Laurussia - North America: Utah, USA	Pyrite framboids and rock geochemistry	Mudstones, cherts, and shales	Pyrite framboids and rock geochemistry	Mudstones, cherts, and shales
16	Siberia: Russia	LKE not exposed	LKE not exposed	Black/ carbonaceous shales and significant pyrites	Dark gray and black carbonaceous-clayey rocks
17	Laurussia - Urals: Russia	Lacking evidences	Limestone, muddy limestone	Trace elements	Limestone
18	Inthanon Zone: Thailand	LKE not exposed	LKE not exposed	Trace elements	Limestone (microbialite)

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#	Locations	LKE		UKE	
		Evidence	Lithology	Evidence	Lithology
19	Sibumasu Terrane: Thailand	None	Limestone	None	Limestone
20	South China: Guangxi, China	Trace elements	Nodular limestone and calcareous turbidites	Trace elements	Nodular limestone and calcareous turbidites
21	Indochina: Vietnam	Trace elements, pyrite framboids	Grey limestone with marls	Trace elements, pyrite framboids	Grey limestone with marls
22	Iran: Iran	Black laminated sandstones	Black laminated sandstones	N/A	N/A

Table D.1 Geological evidences and lithology. Geological evidence and lithology of the LKE and UKE for each location of Table 4.1, based on Carmichael et al. (2019). References are the same as in Table 4.1

D.2 Second scoring method

Performance scores computed using the second formulation of the agreement coefficient A_i (Fig. D.3) are shown in Fig. D.1. Overall, this alternative scoring approach yields perturbation magnitudes for the LKE and UKE that are consistent with those obtained using the first formulation (Fig. D.2), strengthening the inferred nutrient perturbations. Some differences nevertheless emerge. For the LKE, a larger number of simulations reach high performance scores ($\Psi = 0.8$). However, these additional high-scoring simulations are inconsistent with independent constraints that predict a lower seafloor anoxic fraction (Song et al., 2017a; White et al., 2018) (Fig. 4.3), excluding them from providing the best-estimate of the perturbation. For pre-UKE conditions, a performance score of 0.8 is only achieved at $16 \times \text{pCO}_2$. Although this configuration improves overall agreement with the redox dataset, it represents an extreme end-member for atmospheric pCO_2 and does not alter the background $[\text{PO}_4]$. As with the first scoring method, the simulation combining $16 \times \text{pCO}_2$ and $1.25 \times [\text{PO}_4]$ does not provide a plausible representation of the UKE, owing to both unrealistically high pCO_2 and excessive seafloor anoxic fractions. Typically, scenarios involving $16 \times \text{pCO}_2$ were precluded in favour of lower pCO_2

D | Appendix to Chapter 3

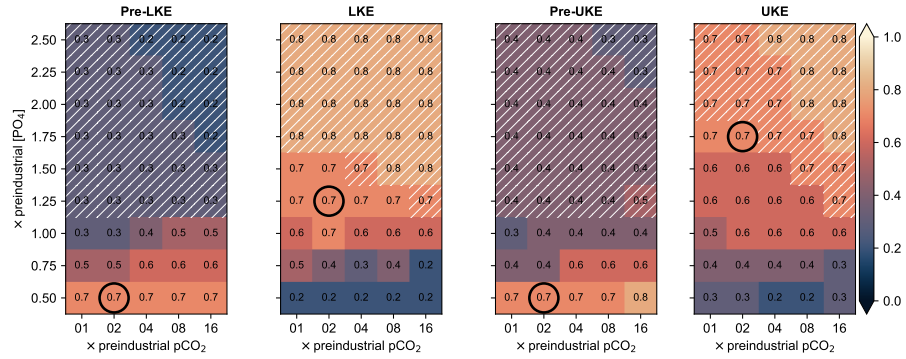


Fig. D.1 *Performance score (Ψ). As in Fig. 4.2, but computed with the second method of agreement coefficients (see Fig. D.3).*

alternatives satisfying the available geological constraints. Overall, estimates of the required perturbation and best-estimate states derived from this second scoring approach converge on the same values as before $0.5\text{--}0.75 \times [\text{PO}_4]$ for the LKE and $1\text{--}1.25 \times [\text{PO}_4]$.

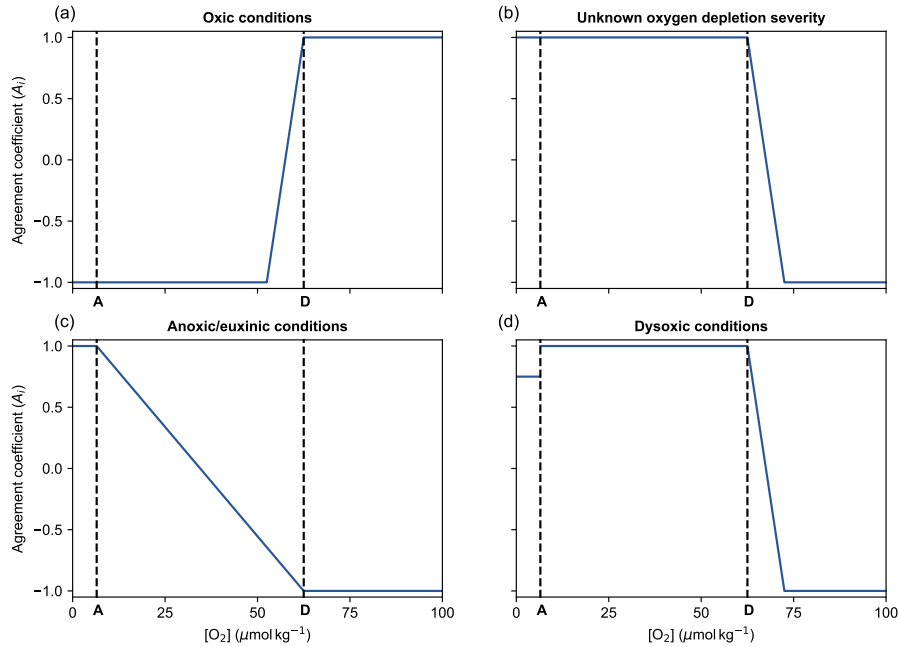


Fig. D.2 Agreement between model and data. Agreement values (A_i) between the model and data depending on the local redox condition (see Table 4.1). These agreement values were used to compute the score from Fig. 4.2. The A and D black dashed lines represent the anoxic and dysoxic thresholds values of 6.5 and $62.5 \mu\text{mol kg}^{-1}$, taken after Sarr et al. (2022).

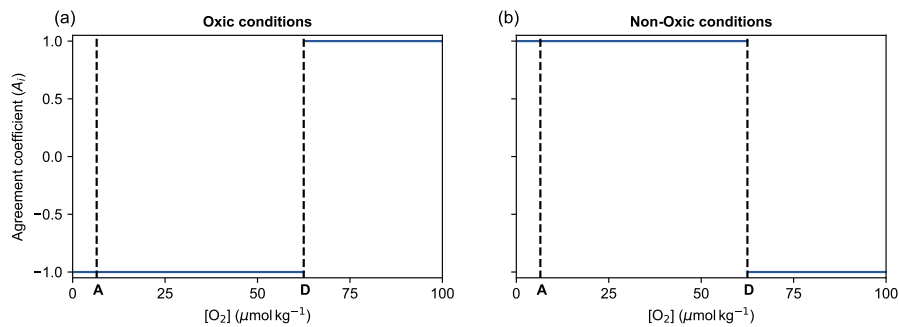


Fig. D.3 Agreement between model and data. As in Fig. D.2, but using a second method to attribute agreement values. These values are used to compute the score from Fig. D.1.

E

List of publications related to the thesis

E.0 First author

- Gérard, J. and Crucifix, M.: **Diagnosing the causes of AMOC slowdown in a coupled model: a cautionary tale**, Earth Syst. Dynam., 15, 293–306, 2024 (*published*). (Appendix A)
- Gérard, J., Sablon, L., Huygh, J. J. C., Da Silva, A.-C., Pohl, A., Vérard, C., and Crucifix, M.: **Exploring the mechanisms of Devonian oceanic anoxia: impact of ocean dynamics, palaeogeography, and orbital forcing**, Clim. Past, 21, 239–260, 2025 (*published*). (Chapter 2)
- Gérard, J., Pohl, A., Sablon, L., Huygh, J., Da Silva, A.-C., and Crucifix, M.: **Spatially contrasted response of Devonian anoxia to astronomical forcing**, EGU sphere, 2026 (*published*). (Chapter 3)

E.0 Co-author

- Sablon, L., Maffre, P., Godd  ris, Y., Valdes, P. J., G  rard, J., Huygh, J. J. C., Da Silva, A.-C., and Crucifix, M.: **An emulator-based modelling framework for studying astronomical controls on ocean anoxia with an application to the Devonian**, Geosci. Model Dev., 18, 10095–10117, 2025 (*published*).
- Huygh, J. J. C., Algeo, T. J., Sageman, B. B., Arts, M., Ver Straeten, C. A., Over, D. J., G  rard, J., Sablon, L., Crucifix, M., and Da Silva, A.-C.: **Astronomical control on marine anoxia during the Kellwasser Crisis and Rhinestreet Event (Appalachian Basin, New York, USA)**, Global and Planetary Change, p. 105216, 2025 (*published*).
- Laridon, A., Couplet, V., G  rard, J., Thiery, W., and Crucifix, M.: **Connecting complex and simplified models of tipping elements: a nonlinear two-forcing emulator for the Atlantic meridional overturning circulation**, Open Research Europe, 2025 (*published*).

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