

Idealized Earth system model analysis of the primary controls on shallow seafloor oxygenation

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Abstract

Key components of the Earth system, including climate, atmospheric oxygen, the strength of the biological pump, and continental configuration, have varied substantially through time. How these factors might have interacted to shape the evolution of marine life—particularly the availability of viable animal habitat—remains unclear. Here, we apply an Earth system model to investigate how tectonic and environmental factors interact to affect the availability of oxic shallow seafloor habitats. We use three idealized continental configurations and run ensembles of model simulations with varying atmospheric CO₂ and O₂, as well as organic matter sinking rates, to assess their coupled influence on seafloor oxygenation. While the dominant control on benthic oxygenation is the partial pressure of oxygen in the atmosphere (pO_2), we find that the efficiency of the biological pump and continental configuration exert strong secondary influences, both directly and through nonlinear interactions. In contrast, atmospheric CO₂ has

only a weak direct effect, influencing benthic oxygenation primarily through interactions with other drivers. We further show that the sensitivity of seafloor anoxia to environmental perturbations is strongly state-dependent, with the largest responses to changes in organic matter sinking rate occurring at intermediate atmospheric pO_2 , and that ocean structure plays a key role in modulating this sensitivity. Our model results highlight the importance of the interaction of multiple boundary conditions for understanding marine oxygenation. The idealized model worlds presented here provide a framework for addressing broader questions of how different Earth system states have shaped the history of life, and vice versa.

1. Introduction

A long-standing idea in ecology is that the size and spatial distribution of available habitat influence species richness, with larger habitats generally supporting more diverse ecosystems (MacArthur & Wilson, 1963). This simple framework has been widely applied to modern systems and has proven remarkably powerful for explaining large-scale biodiversity patterns through changes in habitat availability (e.g., Valente et al., 2020; Tittensor et al., 2010; Jetz & Fine, 2012). Paleontologists have long sought to extend these ecological principles to the fossil record, including to explain dramatic changes in marine diversity throughout the Phanerozoic (Sepkoski, 1997). Earlier studies have tested a range of potential controls on marine diversity over time, including various proxies of rock volume and outcrop area (as proxies for sampling and preservation), the extent of shallow marine environments, sea level, coastline geometry, and continental fragmentation and coalescence (e.g., Raup, 1976; Sepkoski, 1976; Flessa & Sepkoski, 1978; Valentine & Jablonski, 1991; Barnosky et al., 2005; Holland, 2012; Zaffos et al., 2018; Cermeño et al., 2022). These approaches are often based on the hypothesis

that plate tectonics are a key regulator of ancient habitat availability (Valentine & Moores, 1970; Bush & Payne, 2021). However, most studies have failed to find compelling evidence that changes in habitat size and fragmentation alone can fully explain observed patterns in marine biodiversity through the Phanerozoic.

One possible explanation is that habitat availability in the marine realm is not simply a matter of total shallow seafloor area. For metazoans, oxygen availability is a critical determinant of habitability (Nursall, 1959; Tostevin et al., 2016; Reinhard et al., 2016, Sperling et al., 2016; Cole et al., 2020; Sampaio et al., 2021) because it limits the range of many marine organisms and, in conjunction with temperature, is vital in meeting their metabolic demands, both today and in the geologic past (Pohl et al., 2023; Stockey et al., 2021; Deutsch et al., 2015; 2020; Penn et al., 2018; Boag et al., 2018). The exclusion of this factor may account for the failure to find a consistent correlation between habitat area and diversity in the fossil record (e.g., Rasmussen et al. 2019).

Determining the spatial extent of well-oxygenated marine habitat through time is complicated by the fact that multiple interacting factors determine oxygenation of the marine realm (Lyons et al., 2014; Lenton et al., 2014; Fakhraee et al., 2020, Pohl et al., 2022). This study focuses on four main factors—continental configuration, global temperature, atmospheric oxygenation, and the strength of the biological pump—which constitute tectonic and environmental controls on marine habitability. These factors are all known to affect ocean oxygenation and even each other (Fig. 1; Lu et al., 2018; Stockey et al., 2021; Meyer et al., 2016; Reinhard & Planavsky, 2022). Oxygenation of surface waters, for example, is not only dependent on atmospheric oxygen concentrations but also mediated by ambient temperatures, which affect the solubility and bioavailability of oxygen in water (e.g., Boag et al., 2018). The

decay, or remineralization, of organic matter sinking from the surface to the deep ocean is another major factor determining oxygen availability in underlying waters (Meyer et al., 2016). The strength of this process, known as the biological pump, likely has changed through time due to the evolution of marine plankton (Butterfield, 2009; Lenton et al., 2014; Lu et al., 2018) and fluctuations in global temperature, given the temperature-dependence of microbial metabolisms (e.g., John et al., 2014; Hülse et al., 2021). Meanwhile, changes in continental configuration not only alter the distribution of shelf environments but also reshape ocean circulation patterns and, in turn, ventilation, deep-water aging, marine temperature, and mixed-layer nutrient availability—all of which ultimately influence the amount and distribution of oxygen in the ocean (e.g., Donnadieu et al., 2016; Pohl et al., 2022).

Despite the recognized importance of these controls, uncertainty remains regarding their relative influence on marine oxygenation over geologic time (Reinhard & Planavsky, 2022). Although continental configuration, global temperature, atmospheric oxygenation, and the strength of the biological pump have all varied through time due to plate tectonics, volcanism, and biological innovations, the timing and magnitude of these changes remain poorly constrained (e.g., Knoll & Nowak, 2017; Wallace et al., 2017; Scotese et al., 2021). As a result, it remains unclear how strongly each of these factors -- and their interactions -- have influenced the extent of oxygenated shallow marine habitats. A critical first step is therefore to quantify the sensitivity of benthic oxygenation to these four drivers and their interactions (Fig. 1).

Here, we utilize a model approach to evaluate the influence of four factors -- continental configuration, atmospheric CO₂ (as a control on global temperature), atmospheric O₂, and the strength of the biological pump -- on oxic habitat availability in the marine realm (cf. Fig. 1). We apply the cGENIE Earth system model configured in three contrasting idealized

continental configurations (Fig. 2) to explore tectonic drivers of marine oxygenation. Idealized worlds have been successfully used in cGENIE before to isolate key Earth system processes and quantify their sensitivities. For example, Vervoort et al. (2026) used similar configurations to explore how astronomical forcing influences the marine organic carbon cycle and its expression in paleoceanographic records, while Hülse & Ridgwell (2025) demonstrated how interactions between organic matter burial and phosphorus cycling can dominate long-term climate regulation. In addition, Meyer et al. (2016) used a comparable modeling framework to investigate how idealized variations in the biological pump affect ocean redox structure. Together, these studies highlight the value of idealized modeling approaches for exploring mechanistic relationships and identifying thresholds and sensitivities in complex Earth system dynamics.

Building on these approaches, we systematically vary atmospheric CO₂, atmospheric O₂, and the sinking rate of particulate organic matter (and hence the strength of the biological pump) across three continental configurations. In total, we created and ran 360 model simulations, comprising 120 combinations of environmental boundary conditions for each configuration. Each simulation was integrated for 10,000 years to ensure that ocean and biogeochemical fields reached equilibrium prior to analysis. To quantify the relative importance of environmental controls on shallow seafloor anoxia, we then applied a linear model-based variance decomposition. Our idealized model results provide an interactive framework for addressing broader questions of how different Earth system states vary in their habitability and overall suitability for marine life.

2. Model description and method

cGENIE consists of a 3-D frictional geostrophic ocean model with biogeochemical cycling, a 2-D atmosphere model with energy and moisture balance, and a dynamic-thermodynamic sea-ice model (Edwards and Marsh, 2005; Marsh et al., 2011, Ridgwell et al., 2007). As an Earth system model of intermediate complexity, cGENIE captures major features of the living Earth system while requiring relatively low computational resources. These features include large-scale ocean circulation and mixing, which control the transport of heat, carbon, oxygen, and nutrients; atmospheric energy and moisture balance; sea-ice formation and melt; and marine biogeochemical cycling, including the biological pump. The model also represents coupling between these components, allowing interactions between physical climate processes and marine biogeochemistry to emerge. Smaller-scale processes, such as mesoscale ocean eddies or detailed ecosystem dynamics, are parameterized rather than explicitly resolved, enabling efficient simulation of long-term Earth system behavior. cGENIE has been tested extensively against modern observations of nutrients, oxygen, and the carbon cycle and employed in numerous studies of climate, biogeochemistry, and biological productivity over a range of time periods (e.g., Ridgwell & Schmidt, 2010; Norris et al., 2013; Crichton et al., 2023 ; Meyer et al., 2016; Lu et al., 2018; Hülse et al., 2019; Reinhard et al. 2020; Stockey et al. 2021).

In this study, we implement the model on a 36 x 36 equal-area horizontal grid in longitude and latitude with 16 logarithmically scaled depth layers in the ocean (similar to GENIE-16 presented by Cao et al., 2009). We make one modification to the physical parameterization compared to Cao et al. (2009): we replace isopycnal/diapycnal mixing with horizontal/vertical mixing to avoid the occurrence of excessively sharp redox gradients in the ocean (Edwards and Shepherd, 2002; van de Velde et al., 2021). The model is climate-sensitive

(5.77 W/m² radiative forcing per doubling of CO₂), with temperature-dependent remineralization rates for sinking organic matter after Crichton et al. (2021). The marine Fe-cycle is configured as in Tagliabue et al. (2016) and Lambert et al. (2021), with PO₄ and Fe co-limitation of biological productivity. All worlds are initialized with modern default values for solar luminosity (1368 W/m²), mean ocean salinity for an ice-free world (33.9 PSU), and dissolved sulfate inventory (29.16 mmol/kg). Zonal-mean planetary albedo is prescribed according to Supplementary Figure 1a, and an intermediate zonal wind stress field is applied according to Supplementary Figure 1b.

2.1 Idealized continental configurations

We configure the Earth system model cGENIE in three different idealized continental configurations, which we refer to as the ‘meridional’ world, ‘equator’ world, and ‘polar’ world. The meridional and polar configurations are similar to those used by Vervoort et al. (2026). Each world features an ocean with a single, large continent in a specific orientation meant to represent three end-member tectonic configurations with regards to their effect on ocean circulation (Fig. 2). In the meridional world, the continent stretches from pole to pole across all latitudes. In the equator world, the continent covers only low latitudes and features an equatorial gateway. In the polar world, the continent covers only high latitudes, centered on the North pole. The continent in each world is surrounded by a continental shelf that steps down in four depth levels of 175 m, 411 m, 729 m, and 1158 m. The rest of the ocean is set to a depth of 3576 m, resulting in ocean volumes that are similar to that of the modern cGENIE configuration (Table S1). The total extent of shallow seafloor differs between configurations, with the equatorial and meridional worlds exhibiting larger shallow seafloor areas than the polar world. Key properties of each world, including ocean volume, ocean surface area, shallow seafloor area, average ocean temperature,

dissolved O_2 and PO_4 concentrations, and total particulate organic carbon (POC) export, are summarized in Table S1. Diagnostic properties of these worlds are presented in Figure 3 (focusing on ocean oxygenation under pre-industrial environmental conditions) and Section S1 of the Supplement (describing surface currents, deep ocean flow, temperature and salinity, nutrients and productivity, ocean oxygen and euxinia, and sea ice). We have included results using cGENIE with a modern continental configuration (after Crichton et al. 2021), in Figures 2 to 3 and Supplementary Figures 2 to 5 to provide a direct comparison of the various physical and biogeochemical attributes of the three idealized model configurations to the world as it is known today. More details on the diagnostic properties of the three idealized worlds are given in the Supplement, while our main results section focuses on the spatial extent and fraction of anoxic shallow seafloor environments (i.e., the seafloor at water depths of 1158 m or less in cGENIE). We focus on this depth regime because relatively shallow marine environments are comparatively well preserved through the Phanerozoic and shape our perception of the history of life (Shaw et al., 2020; Bottjer, 2016).

2.2 Boundary condition experiments

For each of the three idealized continental configurations, we created and ran an ensemble of different model parameter combinations controlling atmospheric pCO_2 values, atmospheric pO_2 values, and organic matter sinking rates (cf. Meyer et al., 2026) to test how these factors interact to affect benthic oxygenation on the continental shelf (i.e., benthic areas at water depths of 1158 m or less in cGENIE). Atmospheric pCO_2 is included as a parameter as a means to change global temperature, with concentrations prescribed at 1, 2, 4, and 8 times the pre-industrial value (278 ppm). Atmospheric pO_2 is set to 0.2, 0.3, 0.4, 0.5, 0.75, and 1 times the

present atmospheric level (1 PAL = 209,500 ppm). Both atmospheric concentrations broadly span ranges consistent with existing proxy constraints for the Phanerozoic and Neoproterozoic (e.g., Mills et al., 2019; Tostevin & Mills, 2020; Reinhard & Planavsky, 2022). To approximate the effect of ecosystem changes over Earth history on the strength of the biological carbon pump (e.g., Fakhraee et al., 2020), and to account for potentially slower particle sinking rates related to smaller primary producers and the absence of planktic calcifiers prior to the Mesozoic (Butterfield, 2009; Meyer et al., 2026; Knoll & Nowak, 2017; Lu et al., 2018), we vary the organic matter sinking rate in cGENIE, with a slower sinking rate resulting in a less effective transport of organic matter from the surface to the deep ocean. We set organic matter sinking rates to 0.2, 0.4, 0.6, 0.8, and 1 times the modern-ocean default rate in cGENIE (125 m/day). This range of values is consistent with previous model applications (Lu et al., 2018) and spans typical sinking speeds observed in the modern ocean (e.g., McDonnell & Buesseler, 2010; Omand et al., 2020). In total, we created 360 parameter combinations, with 120 combinations of environmental conditions for each of our three continental configurations. Each model world is ran for 10,000 years to allow equilibrium to be reached before we assess the effect of these various environmental and tectonic boundary conditions on benthic oxygenation. Modern-like conditions of 1x $p\text{CO}_2$, 1x $p\text{O}_2$, and 1x sinking rate serve as our default environmental boundary conditions.

2.3 Oxic habitat availability analysis

We present results on how our parameterizations of tectonic and environmental factors (i.e., continental configuration, atmospheric $p\text{CO}_2$ levels, atmospheric $p\text{O}_2$ levels, and sinking rates of organic matter) influence the fraction of anoxic area on the benthic continental shelf in

each of the 360 cGENIE model simulations described above. We define anoxic conditions as dissolved O_2 concentrations below $5 \mu\text{mol } O_2/\text{kg}$. Based on Sperling et al. (2013), we also tested other thresholds for anoxia, with no significant change to our results (Supplementary Figure 6). Because the continental configurations differ in total shallow seafloor area (Table S1), the reported anoxia values represent the fraction of the shallow seafloor that is anoxic rather than absolute area. As a result, comparisons between model worlds reflect differences in relative extent and sensitivity, rather than total anoxic area.

To quantify the relative importance of environmental controls on shallow seafloor anoxia, we applied a linear model-based variance decomposition. The fraction of anoxic shallow seafloor area was expressed as a function of atmospheric pO_2 , atmospheric pCO_2 , organic matter sinking rate, and continental configuration (“world”), including all first-order interaction terms. Atmospheric pCO_2 was expressed as $\log_2(pCO_2)$ to reflect the approximately logarithmic dependence of radiative forcing on CO_2 concentration and to ensure equal weighting of successive doublings. All other predictors were included in linear form. Continental configuration was treated as a categorical variable with three levels (equatorial, meridional, and polar).

The full model can be written as:

$$A = \beta_0 + \beta_1 pO_2 + \beta_2 \log_2(pCO_2) + \beta_3 S + \beta_4 W + \text{interactions} + \epsilon$$

where A is the fraction of anoxic shelf area, S is the organic matter sinking rate, W denotes continental configuration, and ϵ is the residual error term. Interaction terms include all pairwise combinations between predictors. All regression coefficients, standard errors, t-statistics, and p-values are given in Supplementary Table S2.

Variance decomposition was performed using analysis of variance (ANOVA), partitioning

the total sum of squares into contributions from individual predictors and their interactions. This approach quantifies how much of the variability in benthic anoxia is explained by each environmental driver, allowing their relative importance to be expressed as a percentage of the total explained variance. Percent contributions (or % variance explained) were calculated by dividing the sum of squares of each term by the total model sum of squares. Here, the sum of squares represents the sum of squared deviations of the model predictions from their mean, providing a measure of the variability explained by the model. The model explains a large fraction of the variance in benthic anoxia ($R^2 = 0.79$), indicating that the selected predictors capture the dominant controls on the system. Residual analysis indicated no systematic deviations from model assumptions (not shown).

3. Results

3.1 General controls on shelf anoxia

Figure 4 shows the anoxic fraction of the shelf environment across all 360 model configurations as a function of pO_2 . This comprehensive view reveals that all four factors tested—continental configuration, atmospheric pCO_2 , atmospheric pO_2 , and sinking rate—influence benthic shelf anoxia in the model ocean, albeit in different ways and with differing sensitivities. Across all worlds and model configurations, benthic shelf anoxia generally declines with increasing pO_2 , whereas higher organic matter sinking rates—by increasing the delivery of organic matter to the seafloor—tend to enhance shelf anoxia (Fig. 4). By contrast, continental configuration, constrains how potentially habitable shallow seafloor environments intersect with the spatial distribution of oxygen minimum zones (OMZs), and thus modulates their sensitivity to changes in the other environmental parameters. Atmospheric pCO_2 has only a weak and non-

linear direct effect on the fraction of seafloor anoxia, as it influences benthic oxygenation primarily through temperature-dependent changes in oxygen solubility and circulation. Unlike atmospheric pO_2 and sinking rate, which directly control oxygen supply and consumption, respectively, the effect of pCO_2 is indirect and therefore comparatively small within the explored parameter space. The relatively large changes imposed in atmospheric pO_2 and sinking rate, which dominate the system response compared to the more gradual, climate-mediated influence of pCO_2 , further diminish the relative importance of pCO_2 .

While higher sinking rates generally promote benthic shelf anoxia (Fig. 4), separating the full set of model results by sinking rate reveals two additional effects (Fig. 5). First, under slow sinking rates and low pO_2 the development of shelf anoxia can be particularly sensitive to changes in atmospheric pO_2 for equator and polar worlds (Fig. 5b, c, e, f, h, i). Second, at intermediate to high sinking rates, the fraction of anoxic shelf environments generally decreases with increasing atmospheric pCO_2 (Fig. 5g–m), whereas at low sinking rates it increases (Fig. 5a–f); exceptions occur in equatorial and polar worlds at the highest sinking rates (e.g., Fig. 5n–o).

Oxygen depth profiles above the shelves help explain these non-linear interactions between pCO_2 and sinking rate. At high sinking rates, a larger fraction of organic matter is transported to depth, promoting widespread seafloor anoxia (Suppl. Fig. 9) and a vertically expanded OMZ (Fig. 6). In the model, this reduces remineralization in the upper water column and enhances oxygen consumption at depth, shifting the locus of respiration downward and expanding low-oxygen waters. As a result, a larger portion of the continental shelf intersects with the OMZ, leading to more extensive benthic anoxia. Elevated pCO_2 increases temperatures, enhancing remineralization higher in the water column and thereby compressing the OMZ

vertically (Fig. 6), which restricts anoxia to shallower shelf regions (Suppl. Fig. 7). Deviations observed in equatorial and polar worlds at the highest sinking rates (Fig. 5n–o) highlight the role of shelf geometry, where the horizontal and vertical distribution of shelf areas can override this general trend. At low sinking rates, the OMZ is already vertically restricted; in this case, $p\text{CO}_2$ -driven warming primarily reduces oxygen solubility, shifting the entire oxygen profile downward and increasing the extent of anoxic shallow seafloor environments.

3.2 The relative importance of environmental controls for shelf anoxia

Variance decomposition reveals that atmospheric $p\text{O}_2$ is the dominant control on benthic shelf anoxia, explaining ~60% of the total variance across all simulations (Fig. 7a). When interaction terms are included, this contribution increases to ~65%, underscoring the importance of such interactions in regulating benthic redox conditions. The efficiency of the biological pump represents the second most important control, accounting for ~25–28% of the variance, indicating that the delivery of degradable organic matter to the seafloor is a key driver of oxygen consumption. In contrast, atmospheric $p\text{CO}_2$ exerts only a minor influence, contributing <1% as a direct effect and ~3% when interactions are included. The remaining variability is associated with continental configuration which explains ~8–11% of the variance and reflects the role of large-scale ocean circulation and geometry in modulating benthic shelf oxygenation. Interactions between parameters account for ~8% of the total variance, indicating that the system is largely governed by first-order controls, with nonlinear coupling playing a secondary, but significant, role. The most important interaction is between continental configuration and atmospheric O_2 (~2.5%, SI Table S2), followed by interactions between $p\text{O}_2$ and sinking rate (~1.9%) and between sinking rate and $p\text{CO}_2$ (~1.5%).

3.3 Differences between continental configurations and shelf anoxia

The relative importance of drivers varies substantially between continental configurations (Fig. 7b), highlighting the role of ocean and shelf geometry as well as circulation in shaping shelf redox sensitivity. Across the tested environmental boundary conditions, simulated benthic shelf anoxia ranges from ~8–80% in meridional worlds, ~20–100% in equator worlds, and 0–100% in the polar worlds, with polar worlds also exhibiting the highest sensitivity in terms of normalized variability (Figure 4, Table 1). In the polar configuration, benthic anoxia is strongly controlled by pO_2 (~78%), with a smaller but still significant contribution from sinking rate (~21%, Fig. 7b). This configuration also shows the largest relative influence of pCO_2 (~9%), although it remains secondary. The equatorial configuration is similarly dominated by pO_2 (~70%), but with a stronger contribution from sinking rate (~33%) and minimal influence of pCO_2 (<1%, Fig. 7b). In contrast, the meridional configuration exhibits a more balanced control, with pO_2 (~56%) and sinking rate (~45%) contributing nearly equally to benthic anoxia.

4. Discussion

4.1 Oxic marine habitat availability and its key controls

For most of the history of life, the marine realm was characterized by substantially lower oxygenation levels than today (Lu et al. 2018, Reinhard & Planavsky, 2022). Geochemical and sedimentological evidence indicates that widespread anoxia persisted throughout the Paleozoic and much of the Mesozoic, lagging behind the oxygenation of the atmosphere. This has important implications for the evolution and ecology of marine ecosystems, as most metazoans require at least some oxygen to survive (Fenchel & Finlay, 1995; Mentel et al., 2016), although

tolerance thresholds vary among taxa (Seibel & Drazen, 2007; Deutsch et al., 2020). Consequently, reduced ocean oxygenation would have limited the extent of habitable seafloor environments, with direct consequences for marine biodiversity and ecosystem structure.

Quantifying the extent and distribution of oxygenated marine habitats through time, however, remains challenging, because oxygenation is governed by multiple interacting Earth system boundary conditions, including atmospheric O_2 and CO_2 , continental configuration, and biological processes (Donnadieu et al. 2016; Lu et al. 2018; Meyer et al. 2016; Pohl et al., 2022; Reinhard & Planavsky 2022). The relative importance of these controls likely varied over geological timescales as these boundary conditions evolved. Recent work has further highlighted that ocean oxygenation cannot be understood as a simple function of atmospheric pO_2 alone. For example, Pohl et al. (2022) demonstrated that continental rearrangements can drive large-scale changes in ocean circulation and ventilation, enabling widespread seafloor anoxia even under modern pO_2 conditions. Similarly, Meyer et al. (2016) demonstrated that the efficiency and vertical structure of the biological pump exert a first-order control on the distribution of oxygen in the ocean, with changes in the depth of organic matter remineralization strongly influencing the prevalence and depth of anoxia.

Our model experiments provide a quantitative framework to evaluate the relative importance and interplay of these controls. Across all simulations within our idealized model worlds, a consistent picture emerges in which benthic anoxia is primarily controlled by atmospheric pO_2 and the efficiency of the biological pump controlling organic matter delivery to the seafloor, with continental configuration modulating the sensitivity to these drivers. This is consistent with the view that atmospheric oxygen sets the upper boundary condition for ocean oxygenation, while circulation and biogeochemical processes determine how this oxygen is

distributed and consumed within the ocean interior (Meyer et al. 2016; Pohl et al., 2022; Reinhard & Planavsky 2022). At the same time, our results support and extend previous findings by showing that continental configuration plays a key role not only in setting the baseline oxygenation state, but also in modulating the system's response to changes in atmospheric and biological forcing. In particular, the strong sensitivity of benthic anoxia to sinking rate in our simulations aligns with previous work demonstrating that changes in the spatial distribution of organic matter remineralization can drive large shifts in marine redox structure (Meyer et al., 2016).

The comparably weak influence of $p\text{CO}_2$ suggests that, within the explored parameter space and our model worlds, temperature-driven changes in productivity, remineralisation, ocean stratification, or oxygen solubility exert only a secondary influence on benthic oxygenation relative to direct controls on oxygen supply and organic matter flux. This does not imply that climate is unimportant, but rather that its effects are expressed primarily through interactions with other drivers and are therefore strongly state-dependent. This interpretation is consistent with previous findings that ocean oxygenation varies strongly with circulation state (Pohl et al., 2022) and that the impact of organic matter remineralization depends on the background system state (Meyer et al., 2016). In addition, the comparatively large changes imposed in atmospheric $p\text{O}_2$ and sinking rate in our experiments dominate the system response, further reducing the apparent influence of $p\text{CO}_2$ relative to these primary controls.

4.2 From model worlds to history of marine life on Earth

The model worlds and scenarios explored here are highly simplified relative to the complexity of Earth system evolution, yet they provide a useful framework for isolating how

shallow seafloor oxygenation responds to changes in key boundary conditions. Several general insights emerge from these experiments:

4.2.1. Benthic habitat availability emerges from coupled environmental and tectonic controls.

Benthic habitat availability likely fluctuated throughout much of the Phanerozoic in response to interacting environmental and tectonic factors beyond atmospheric pO_2 , as evidenced by geological records showing that widespread marine anoxia persisted long after the final oxygenation of the atmosphere (Sperling et al. 2015, Lu et al. 2018, Jenkyns 2010). Consistent with this complexity, our results show that while atmospheric pO_2 is the dominant control on benthic oxygenation, explaining ~60% of the variance directly and ~65% when interactions with other parameters are included (SI Table 3), organic matter sinking rate and continental configuration exert strong secondary influences, both directly and through interactions.

The dominant interaction between pO_2 and continental configuration (explaining ~2.5% of the variance, SI Table 3) highlights that ocean structure controls how dissolved oxygen is distributed within the ocean, such that the sensitivity of benthic anoxia to oxygen availability varies significantly between different circulation regimes. The pO_2 – sinking rate interaction (~1.9%) reflects the coupling between oxygen supply and demand through organic matter degradation, whereby the effect of enhanced organic carbon flux to the seafloor on benthic anoxia is stronger under low-oxygen conditions as indicated by the negative pO_2 –sinking interaction term (Table S2) and the increased variability in anoxia at low to intermediate pO_2 (Fig. 4). Mechanistically, this indicates that the same increase in sinking rate and thus organic matter delivery to the seafloor can lead to different benthic oxygenation outcomes depending on background oxygen availability: under low pO_2 , limited oxygen supply cannot offset increased

408 respiration at the seafloor, promoting widespread anoxia, whereas under high pO_2 , enhanced
409 oxygen supply can buffer increased respiration.

410 Finally, all pCO_2 interactions -- specifically with sinking rate ($\sim 1.5\%$), continental
411 configuration ($\sim 0.9\%$), and pO_2 ($\sim 0.7\%$) -- exceed the direct influence of pCO_2 ($< 0.01\%$),
412 indicating that temperature affects benthic anoxia primarily through indirect pathways.
413 Mechanistically, this reflects temperature-driven changes in organic matter remineralization
414 depth, as well as ocean circulation and stratification, which together control where organic
415 matter is respired and how oxygen is distributed in the ocean interior. As a result, the influence
416 of climate on seafloor anoxia is expressed through its modulation of both oxygen supply and
417 demand, rather than as a direct control. Together, these effects indicate that benthic habitat
418 availability is not solely determined by atmospheric oxygen, but by the interplay between oxygen
419 supply, organic matter flux, and ocean geometry.

420 We note that the influence of continental configuration may be amplified in our idealized
421 model worlds, where simplified geometries may promote deep mixed layers, strong upwelling,
422 or expanded oxygen minimum zones (Figure 2, 3; Supplementary Figure 2, 4; see Section S1 of
423 the Supplementary Material). These features may exaggerate the sensitivity of anoxia relative to
424 the real ocean. Nevertheless, we propose that the simulated coupling between tectonic and
425 environmental controls, and their shifting relative importance, represents a robust feature of the
426 Earth system.

427

428 4.2.2. *Biological evolution and its context-dependent impact on shelf oxygenation*

429 The evolution of larger and more complex plankton ecosystems, and a more efficient
430 biological pump, is often assumed to enhance oxygenation of shallow marine environments by

shifting organic matter degradation to greater depths (Logan et al., 1995; Fakhraee et al., 2020). While this holds for the pelagic ocean (Meyer et al., 2016), our results show that increased sinking rates generally promote benthic anoxia on continental shelves, as a greater flux of organic matter reaches the seafloor and enhances oxygen consumption. The magnitude of this effect, however, depends on environmental context, particularly atmospheric pO_2 and continental configuration (e.g., Fig. 4).

The significant pO_2 –sinking interaction (~1.9%, SI Table 3) indicates that the impact of changes in biological pump efficiency depends on background oxygen conditions. Rather than exerting a uniform influence, increases in sinking rate produce the largest changes in shelf anoxia at intermediate pO_2 , as reflected in the elevated variability across simulations (Fig. 4, SI Table 4), while their effect is substantially muted under well-oxygenated conditions.

This state dependence has important implications for interpreting the role of biological evolution in shaping marine oxygenation. Increases in biological pump efficiency, for example associated with the evolution of larger and/or mineralized plankton causing higher sinking rates (e.g., Logan et al., 1995; Butterfield, 2009; Falkowski et al., 2004), would have had the greatest impact on shallow seafloor redox conditions during intervals of intermediate atmospheric oxygenation, when oxygen supply and demand were more closely balanced. Under these conditions, relatively small changes in organic matter sinking rate could drive large expansions or contractions of anoxic shallow seafloor environments. In contrast, under highly oxygenated conditions, enhanced oxygen supply would buffer increases in respiration, limiting the expansion of seafloor anoxia.

The magnitude of this effect is further modulated by ocean structure, as reflected in differences between continental configurations (Fig. 4). Together, these results indicate that the

impact of biological evolution on shallow seafloor oxygenation was state-dependent, with greatest sensitivity occurring under intermediate oxygenation, like those of the Paleozoic to early Mesozoic, and a reduced sensitivity under the highly oxygenated conditions of the last ninety million years.

4.2.3. Ocean structure controls the sensitivity of shelf oxygenation to environmental change.

Differences between continental configurations demonstrate that ocean geometry and circulation fundamentally control how shelf oxygenation responds to environmental forcing (Table 1). This reflects not only differences in total shelf area, but also how shallow seafloor environments intersect with OMZs, ventilation pathways, and regions of organic matter remineralization. Thus, the same change in atmospheric pO_2 or biological pump efficiency can produce different benthic oxygenation responses depending on where shelves are located relative to low-oxygen water masses.

The polar configuration exhibits the highest sensitivity, both in terms of absolute variability and normalized response, with small changes in pO_2 and biological pump efficiency producing large changes in benthic anoxia (e.g., Fig. 4). Its high pO_2 sensitivity likely reflects ventilation-limited conditions (see Fig.2c and S1.2 in Supplement), where reduced deep-water formation or restricted exchange makes benthic oxygenation especially dependent on the atmospheric oxygen boundary condition. In this case, changes in pO_2 directly alter the amount of oxygen available to ventilate shelf and subsurface waters, whereas changes in sinking rate have a smaller relative effect because shelf oxygenation is already strongly constrained by oxygen supply. The polar world also shows the largest relative influence of pCO_2 (~9%), likely reflecting the enhanced sensitivity of high-latitude shallow seafloor environments to temperature-driven

changes in oxygen solubility, organic matter remineralization, and stratification.

In contrast, the meridional configuration displays lower overall sensitivity but a more balanced control, with pO_2 and sinking rate contributing nearly equally to the observed variance in benthic anoxia (Table 1). One explanation is that shallow seafloor environments in this configuration intersect more strongly with regions where OMZ expansion or contraction is sensitive to organic matter flux (SI Fig. 4). Increasing sinking rate therefore expands low-oxygen waters onto shelf depths (SI Fig. 9), making biological pump efficiency particularly important. Nutrient recycling likely further reinforces this response by sustaining productivity and organic matter export in regions connected to the shelves, although we have not directly diagnosed this mechanism in the model output.

The equatorial configuration occupies an intermediate regime: benthic anoxia is strongly controlled by pO_2 , but sinking rate also contributes substantially (Table 1). This is consistent with enhanced productivity and recycling in low-latitude systems, where changes in organic matter export affect oxygen demand, but the overall extent of anoxia remains strongly constrained by atmospheric oxygen availability.

Together, these results suggest that continental configuration controls not only the mean extent of shallow seafloor anoxia, but also the relative importance of different environmental drivers. In particular, shallow seafloor oxygenation depends on how ocean circulation, OMZ structure, nutrient cycling, and shelf geometry combine to determine whether changes in oxygen supply or organic matter delivery dominate the response.

5. Conclusion

Using idealized model worlds, we present a mechanistic framework for investigating how

500 abiotic and biotic factors may have jointly controlled the oxygenation of shallow seafloor animal
501 habitats throughout Earth history. Across all simulations, benthic shelf anoxia is primarily
502 determined by atmospheric pO_2 , with biological pump efficiency exerting a strong secondary
503 influence, reflecting the balance between oxygen supply and demand through organic matter
504 respiration. By contrast, atmospheric pCO_2 has only a weak direct effect, influencing shallow
505 seafloor oxygenation mainly through interactions with other drivers.

506 Beyond these first-order controls, our results highlight the importance of state-dependent
507 and nonlinear responses. Interactions between parameters -- particularly between continental
508 configuration and pO_2 , and between pO_2 and sinking rate -- indicate that benthic oxygenation is
509 strongly controlled by the interplay of shelf distribution, ocean structure, ambient oxygen, and
510 the efficiency of the biological pump. Consistent with this, ~20% of the variance in benthic
511 anoxia remains unexplained by the linear statistical model used to quantify the effects of
512 environmental drivers, indicating that nonlinear and state-dependent processes play a substantial
513 role in shaping shallow seafloor redox conditions.

514 The importance of interactions between environmental parameters has key implications
515 for interpreting Earth history. In particular, the pO_2 -sinking rate interaction implies that the
516 impact of biological pump efficiency is maximized at intermediate oxygenation states, when
517 oxygen supply and demand are closely balanced. Under such conditions, evolutionary
518 innovations that enhance or reduce organic matter export -- such as the emergence of larger or
519 mineralized plankton, or more efficient microbial recycling -- could drive large shifts in benthic
520 redox conditions, whereas their impact would be dampened under highly oxygenated conditions.

521 More broadly, our results suggest that changes in temperature alone were unlikely to drive
522 major shifts in benthic oxygenation unless coupled with changes in ocean circulation or

biological pump efficiency. Instead, the extent of anoxic and oxic shallow seafloor environments likely emerged from the co-evolution of these boundary conditions, with climate acting primarily to amplify or dampen oxygenation states set by oxygen availability and organic matter flux. In this framework, atmospheric pO_2 sets the upper bound for ocean oxygenation, while ocean and shelf geometry regulate how strongly benthic oxygenation respond to changes in carbon cycling, climate, and biological evolution. Together, these processes help to explain how the extent of habitable seafloor may have varied through time, providing an environmental context for marine ecosystem evolution.

Tables

Table 1 Per-world sensitivity of shallow seafloor anoxia. Total anoxia range shows the minimum–maximum fraction (%) of anoxic shallow seafloor across simulations. The coefficient of variation ($CV=\mu/\sigma$) quantifies relative variability in anoxia within each world. Parameter importance (% variance explained) indicates the relative contribution of each driver to anoxia variability, including interaction effects, and therefore sum to > 100%.

World	Total Anoxia Range	Coefficient of Variation	Parameter importance (% variance explained)		
			pO_2	Sinking	pCO_2
Meridional	8 - 80%	0.60	56.3	45.0	2.8
Equator	20 - 100%	0.56	70.2	33.2	0.9
Polar	0 - 100%	1.03	78.2	21.2	8.9

Figures

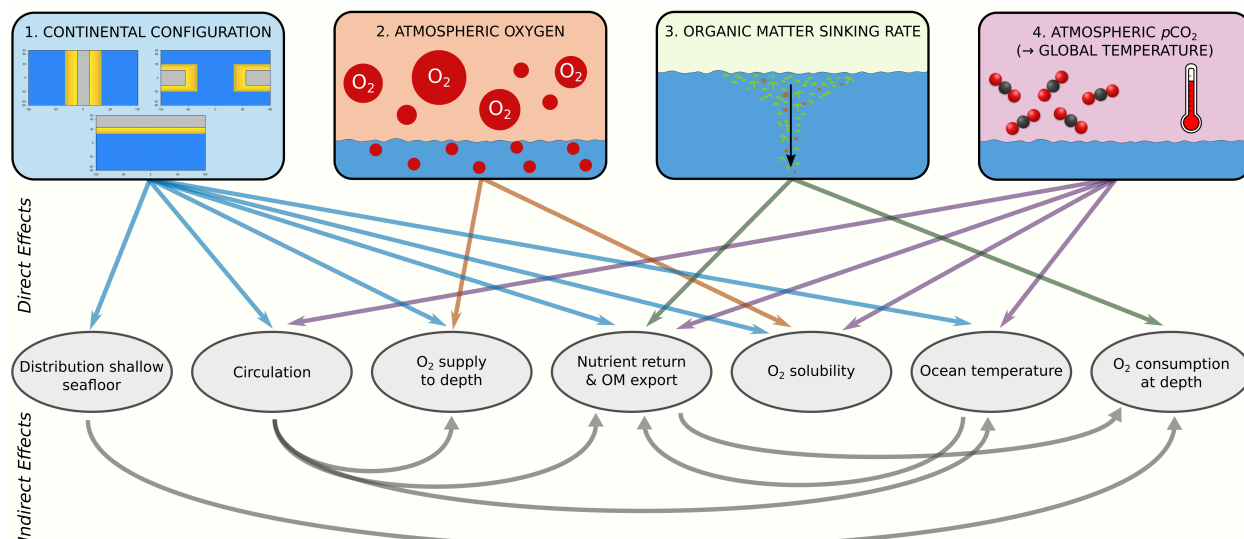


Figure 1. Conceptual schematic of the controls on shallow seafloor anoxia. The diagram illustrates the direct and indirect interactions between four primary drivers -- continental configuration, atmospheric O₂, the sinking rate of organic matter (biological pump strength), and atmospheric pCO₂ (via its control on global temperature) -- and the key physical and biogeochemical processes that regulate shallow seafloor oxygenation. Colored arrows denote direct effects of each driver on these processes, while grey arrows indicate indirect effects resulting from interactions among these processes. Together, these coupled pathways determine the spatial distribution and extent of anoxic conditions on the shallow seafloor.

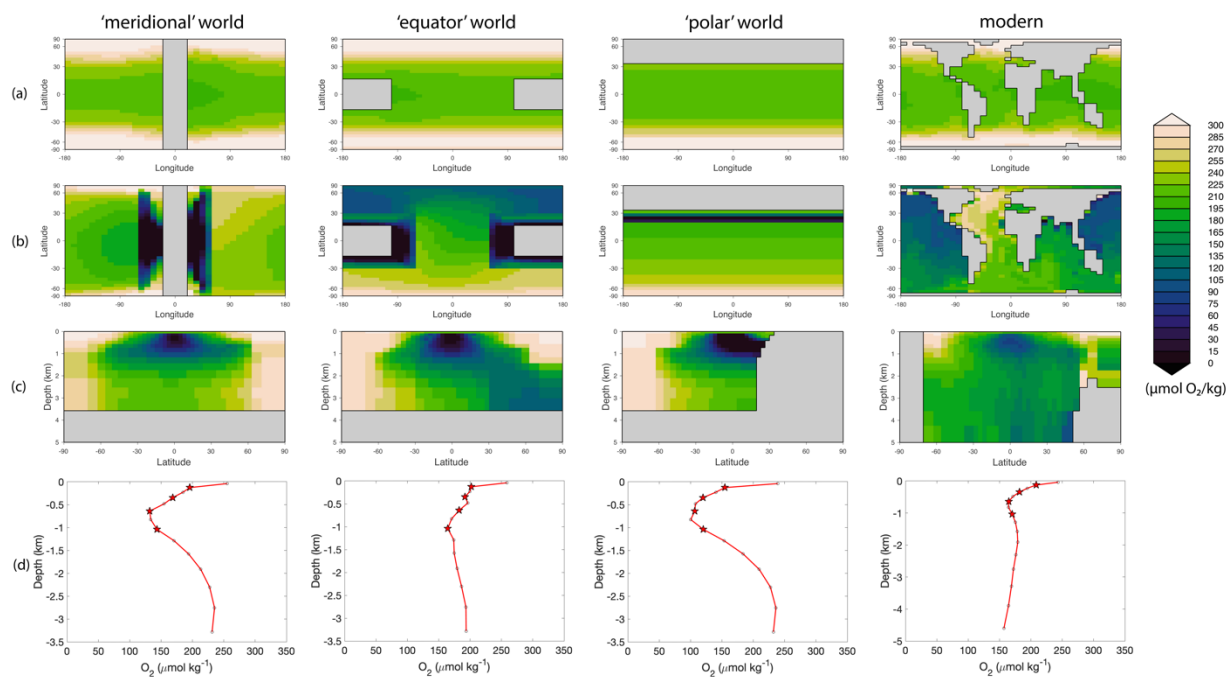
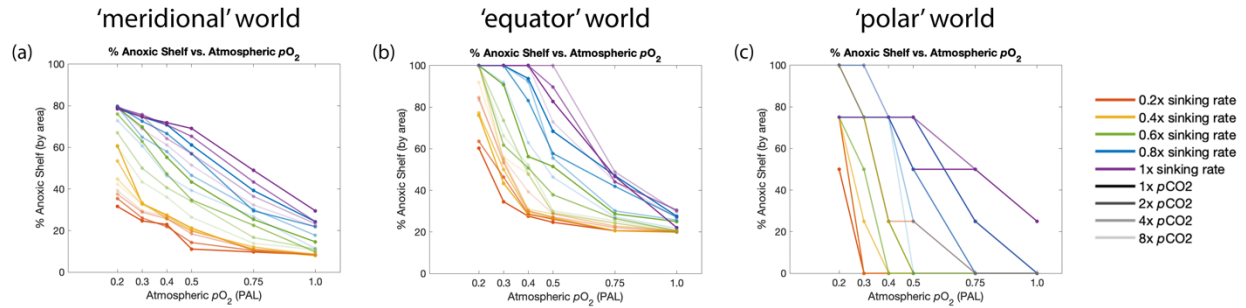


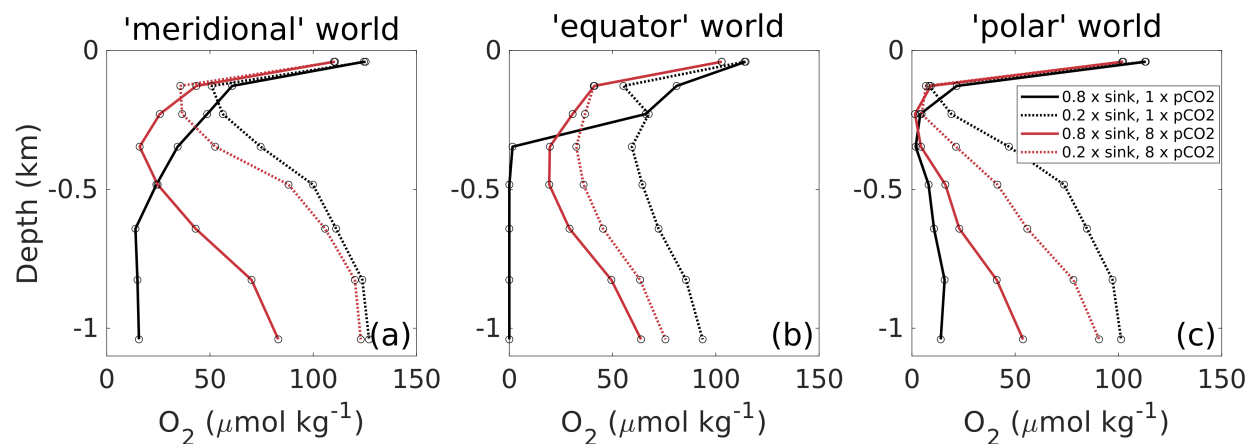
Figure 3: Ocean oxygen concentrations for the three model worlds compared to modern under default environmental conditions (i.e., pre-industrial $p\text{CO}_2 = 278$ ppm, modern $p\text{O}_2$ at 100% PAL, and modern sinking rate at 125 m/day). Panels show oxygen concentrations at (a) the surface, (b) the seafloor, (c) zonally averaged vertical profiles, and (d) global profiles, with stars in (d) indicating oxygen concentrations at the four continental shelf depth levels.



568
 569 **Figure 4: Fraction of anoxic benthic shelf area for model configurations in (a) the**
 570 **meridional world, (b) the equator world, and (c) the polar world.** Each point represents a
 571 single model experiment. Points representing experiments with the same sinking rate and pCO_2
 572 are connected by lines. The y-coordinate shows the percentage of the continental shelf that is
 573 anoxic (i.e., $< 5 \mu\text{mol } O_2/\text{kg}$).

Figure 5: Fraction of anoxic benthic shelf area for all model configurations separated by sinking rate in the meridional world (left), equator world (middle), and polar world (right). As in figure 4, each point represents a single model experiment. Points representing experiments with the same sinking rate and $p\text{CO}_2$ are connected by lines. The y-coordinate shows the percentage of the continental shelf that is anoxic (i.e., $< 5 \mu\text{mol O}_2/\text{kg}$). The shaded polygon in each panel shows the full range of results from all 120 experiments in the idealized world.

584



585 **Figure 6: Oxygen depth profiles over continental shelf environments** in the ‘meridional’ (a),
586 ‘equator’ (b), and ‘polar’ (c) worlds under $0.5\times$ modern $p\text{O}_2$. Profiles are shown for contrasting
587 sinking rates and atmospheric $p\text{CO}_2$ levels (see legend), illustrating the influence of these
588 parameters on water-column oxygen structure.

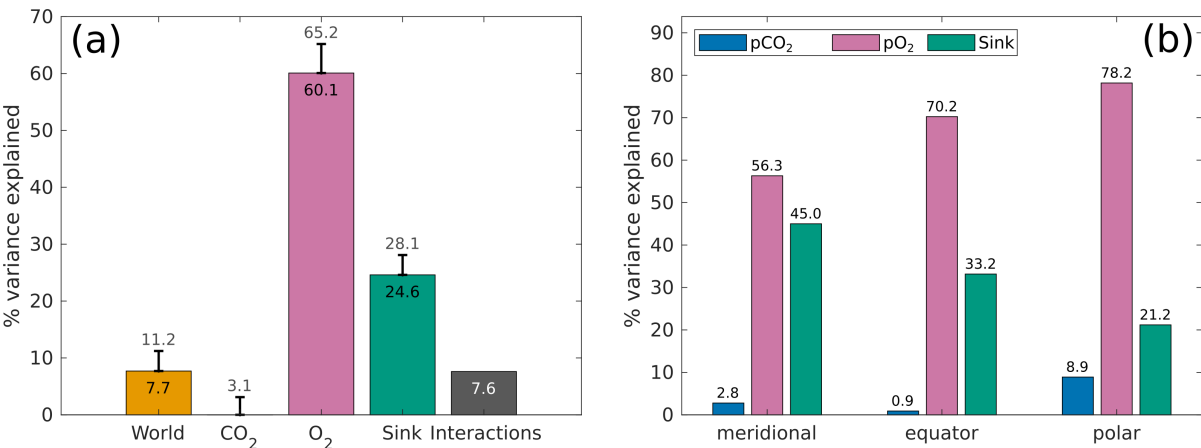


Figure 7: Variance decomposition based on linear models with interaction terms across all experiments (a) and per model worlds (b). Bars in (a) indicate the contribution of main effects and the sum of all interactions to explained variance, while error bars represent the additional contribution from interaction terms. Bars in (b) indicate the contribution of main effects and additional contributions from interactions.

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Supplementary Material to Idealized Earth system model analysis of the primary controls on shallow seafloor oxygenation

Supplement

S1. Diagnostic properties of model worlds at default environmental conditions

Here we discuss simulation results for our three idealized worlds—meridional world, equator world, and polar world—at default environmental boundary conditions of 1x $p\text{CO}_2$, 1x $p\text{O}_2$, and 1x sinking rate. These parameters are described in Section 2.2 of the main text. We often reference details from the ‘modern’ world, which refers not to the real-life ocean but the model representation of it in cGENIE, after Crichton et al. (2021).

S1.1 Surface currents

The meridional world most closely resembles our modern ocean in terms of surface ocean circulation, with clear subtropical and subpolar gyres (Figure 1c) and surface currents extending a few hundred meters in depth (~400 m, Figure 1c). In contrast, the equator and polar worlds feature distinct high-speed circumglobal currents (two in the equator world at ~60°N and ~60°S and one in the polar world at ~60°S) and surface currents that extend markedly deeper (~1200 and ~800 m deep in the equator and polar worlds, respectively). The vertical extent of surface currents in the meridional world is comparable to the depth of most surface currents in the modern world (~400 m), while surface currents in the equator and polar worlds show more similarity to modern surface currents in the Southern Ocean where they can reach ~800 m or

even lower. Surface currents may extend more deeply in the idealized worlds due to more aggressive mixing caused by a combination of a simplified applied wind field and vertical/horizontal, rather than isopycnal/diopycnal, mixing.

The two idealized worlds with circumglobal currents have higher maximum surface current speeds closer to that of the modern world (equator - 0.081 m/s, polar - 0.080 m/s, modern - 0.086 m/s) than the meridional world, which features no circumglobal current (meridional - 0.070 m/s). The equator and polar worlds also have higher mean surface current speeds (equator - 0.027 m/s; polar - 0.031 m/s) than the meridional world, though ultimately all are roughly comparable to similarly gridded data in the modern (meridional - 0.024 m/s; modern - 0.025 m/s).

S1.2 Deep ocean flow

Vertical cross-sections of global streamfunction in the model oceans show varying patterns of deep ocean flow for all worlds (Figure 1c). In the meridional world, water subducts at both poles and upwells near the equator, forming two distinct partitions of water that flow in opposite directions beneath the surface currents. The position of the continent in the meridional world ensures that northward and southward flows of deep water are relatively uninterrupted. In the equator world, deep ocean flow is complicated by the presence of a continent between $\sim 30^\circ\text{N}$ and $\sim 30^\circ\text{S}$, with an open equatorial gateway that spans $\sim 60^\circ\text{W}$ to $\sim 60^\circ\text{E}$. Perhaps due to the continental configuration, surface currents at $\sim 45^\circ\text{N}$ as well as $\sim 45^\circ\text{S}$ extend more deeply as they hit the continental shelf. The strong mixing that results from such currents may disrupt deep ocean flows. In the equator world, water subducts in the south pole and upwells at the equator, but the flow is much weaker and less direct than that found in the meridional world. The northern

hemisphere ocean displays strong subduction at the north pole (more intense than that found at the south pole) and similarly weak upwelling at the equator. Finally, deep ocean flow in the polar world is limited by the placement of a continent covering a large section of the northern hemisphere, extending from the north pole down to $\sim 30^{\circ}\text{N}$ or $\sim 15^{\circ}\text{N}$ depending on the depth at which subsurface waters are interacting with the continental shelf. In the polar world there is one prominent movement of water, subducting at the south pole and upwelling at the equator.

S1.3 Temperature and salinity

Mean global ocean temperatures for the meridional, equator, and polar worlds are within 2°C of the mean global ocean temperature for the modern world (meridional - 1.9°C ; polar - 2.9°C ; equator - 4.1°C ; modern - 3.6°C). Latitudinal temperature gradients in the three idealized worlds are comparable to those found in the modern, with slightly lower average temperatures at both the poles and the equator. Temperatures range from -1.7°C at the equator to 25.2°C at the poles (averaged longitudinally) in the meridional world, -1.9°C to 25.8°C in the equator world, -1.9°C to 26.3°C in the polar world, and -1.5°C to 27.2°C in the modern world. Overall, the meridional world experiences the coldest temperatures and narrowest temperature range of all the idealized worlds, while the equator world experiences the warmest temperatures and widest temperature range. In all idealized worlds, the ocean is characterized by warmer surface waters centered at the equator and near-freezing temperatures everywhere else (Supplementary Figure 2a). The vertical extent of these warmer surface waters differs among all three worlds, much like the vertical extent of the surface currents. In the meridional world, temperatures above $\sim 10^{\circ}\text{C}$ occur as deep as ~ 500 m, while the equator and polar worlds feature elevated temperatures as deep as ~ 800 m.

The meridional, equator, and polar worlds experience a narrower range of salinities than the modern world. While maximum salinities are comparable (meridional - 35.3 PSU; equator - 35.6 PSU; polar - 35.4 PSU; modern - 35.5 PSU), the idealized worlds have higher minimum salinities than the modern (meridional - 34.5 PSU; equator - 34.4 PSU; polar - 34.3 PSU; modern - 32.3 PSU). In all idealized worlds, highest salinities are found in low latitudes near the equator and lowest salinities are found in high latitudes near the poles (Supplementary Figure 2). In the meridional world, salinity gradients are roughly symmetrical between the northern and southern hemispheres. Pools of saltier water exist between 60°N and 60°S of the equator, and they extend down to ~800 m in the ocean. Meanwhile, pools of less salty water exist near both poles and extend down to ~400 m in the ocean. These patterns are likely due to relatively even subduction of polar water and upwelling near the equator in both hemispheres. In contrast, the ‘equator’ and ‘polar’ worlds show greater differences in the distribution of salinity between hemispheres. In the equator world, fresher water at the poles extends more deeply and more southward in the northern hemisphere, while saltier water near the equator extends more deeply and more southward in the southern hemisphere. This disparity may reflect the equator world’s asymmetrical deep ocean flow patterns (e.g., particularly strong subduction in the north pole). A similar pattern is found in the polar world, where saltier waters are deeper and more extensive in the southern hemisphere than the north. In contrast, however, fresh waters are restricted in the northern hemisphere to just above the top two steps of the continental shelf.

S1.4 Nutrients and productivity

PO₄ concentrations in the meridional, equator, and polar worlds are noticeably higher and more wide-ranging than in the modern world (Supplementary Figure 2, 3). In the meridional

world, nutrients are most concentrated at the equator near the surface, reaching a maximum of 3.1 $\mu\text{mol/kg}$ (averaged latitudinally). In the equator world, nutrients are most concentrated in the subpolar region of the northern hemisphere, close to the seafloor, reaching a maximum of 3.0 $\mu\text{mol/kg}$. There are also substantial nutrients at the equator near the surface at concentrations of $\sim 2.7 \mu\text{mol/kg}$. In the polar world, nutrients reach maximum concentrations of 3.4 $\mu\text{mol/kg}$. They are concentrated at the equator near the surface, similar to the meridional world, but also extend northward in subsurface waters and hit the continental shelf. The modern world does not feature comparably high nutrient concentrations so close to the ocean surface. Similarly, productivity, in the form of POC flux (density), appears noticeably higher in the meridional, equator, and polar worlds than in the modern world (Supplementary Figure 2, 3). This may be due to stronger equatorial and continental upwelling in the three idealized worlds than in the modern. Deeper mixing in the idealized worlds may entrain nutrients and POC in the surface ocean rather than allowing them to sink. Excess PO_4 may also result from Fe limitation as productivity in the idealized worlds is both PO_4 - and Fe-limited.

S1.5 Ocean oxygen and euxinia

The meridional, equator, and polar worlds experience much lower minimum O_2 concentrations than the modern world (meridional - 13.0 $\mu\text{mol/kg}$; equator - 2.1 $\mu\text{mol/kg}$; polar 0.0 $\mu\text{mol/kg}$; modern - 85.0 $\mu\text{mol/kg}$), as well as higher maximum H_2S concentrations (meridional - 15.4 $\mu\text{mol/kg}$; equator - 43.5 $\mu\text{mol/kg}$; polar - 78.2 $\mu\text{mol/kg}$; modern - 2.1 $\mu\text{mol/kg}$) (Supplementary Figure 2). The three idealized worlds also feature well-developed and extensive oxygen minimum zones (OMZs), centered below and extending beyond the equatorial upwelling zone (Supplementary Figure 2). The shape and depth of the oxygen minimum zones

are reflective of other patterns in nutrient distribution and ocean circulation. Using a cutoff of $< \sim 100 \mu\text{mol/kg}$ (O_2 values are averaged across longitudes), the OMZ extends from $\sim 20^\circ\text{S}$ to $\sim 20^\circ\text{N}$ and is ~ 1100 m deep in the meridional world. The OMZ extends from $\sim 20^\circ\text{S}$ to $\sim 20^\circ\text{N}$ and is ~ 1300 m deep in the equator world, and extends from $\sim 15^\circ\text{S}$ and $\sim 30^\circ\text{N}$ and is ~ 1300 m deep in the polar world. Meanwhile, the OMZ in the modern world only extends from $\sim 10^\circ\text{S}$ to $\sim 10^\circ\text{N}$ and is ~ 850 m deep. As in the modern world, OMZs are concentrated along the continental shelf of each of the three idealized worlds; however, the three idealized worlds differ in which parts of the shelf are impacted by the OMZ (Supplementary Figure 4). For example, in the equator world, water with $< 15 \mu\text{mol/kg}$ O_2 is found on the top three steps of the continental shelf, while in the polar world, such low-oxygen water only directly interacts with the third step of the continental shelf. Euxinic zones are found at the cores of these OMZs where oxygen is depleted. Overall, the three idealized worlds are characterized by much greater anoxic and euxinic ocean conditions than the modern world, with particularly strong OMZs and euxinic zones found in the equator and polar worlds.

S1.6 Sea ice

Each of the idealized worlds feature roughly 5 to 10% surface sea ice cover (Supplementary Figure 5a). The most extensive sea ice cover is found in the equator world (11.1% of surface grid cells contain some amount of sea ice), followed by the meridional world (8.0%), and polar world (5.6%). The thickest sea ice is found in the meridional world, reaching up to 5 m thick, in comparison to maximums of ~ 4 m in other worlds (Supplementary Figure 5b). In all idealized model worlds, except the equator world, sea ice cover reduces to 0% at $4\times \text{CO}_2$ (1112 ppm). Sea ice cover is 0% for all idealized model worlds at $8\times \text{CO}_2$ (2224 ppm).

Particulate organic carbon flux (POC) is negligible throughout the water column under sea ice, due to the model assumption of no productivity under the ice.

For ease of discussion of these 360 possible model configurations, we choose one continental configuration and one combination of environmental factors as our default, or base, simulations to examine in detail before introducing other simulations for comparison and contrast. We treat the meridional world as our default continental configuration because its continental shelf spans the full range of latitudes and features the widest diversity of potential habitat.

S2. Linear model–based variance decomposition

S2.1 Regression coefficients and statistical interpretation

Table S2 summarizes the estimated regression coefficients and associated uncertainties for all main effects and interaction terms. The coefficients are consistent with the variance decomposition results and provide additional insight into the direction and strength of individual effects. Atmospheric pO_2 exhibits a strong negative coefficient, confirming its dominant role in limiting benthic anoxia through enhanced oxygen supply. In contrast, organic matter sinking rate shows a large positive coefficient, indicating that increased carbon flux to the seafloor substantially enhances oxygen consumption and promotes anoxia. Atmospheric pCO_2 also has a statistically significant positive coefficient, but its magnitude is smaller, consistent with its more limited direct contribution to variance. Several interaction terms are significant and highlight key nonlinear couplings. Overall, the regression coefficients reinforce the interpretation that benthic anoxia is primarily governed by the balance between oxygen supply and organic matter respiration, with secondary modulation by ocean structure and weaker, indirect effects of

165 atmospheric CO₂.

166

167 *S2.2 Notes on interpretation*

168 It is important to note that the purpose of this analysis is not hypothesis testing in a
169 classical statistical sense, but rather the quantification of relative driver importance within a
170 structured model ensemble. Accordingly, emphasis is placed on variance contributions and effect
171 sizes rather than statistical significance alone. The linear model provides a useful and
172 interpretable approximation of the system behavior, capturing both first-order controls and
173 leading-order interactions.

Supplementary Table

	Ocean volume (km ³)	Ocean surface area (km ²)	Shallow seafloor area (km ²)	Average ocean temperature (°C)	Average ocean O ₂ (μmol/kg)	Average ocean PO ₄ (μmol/kg)	Total POC export (Pg C/yr)
'meridional' world	1,285,507,000	453,248,300	113,310,000	1.9	197	2.2	14
'equator' world	1,286,760,000	446,953,200	107,020,000	2.9	187	2.2	15
'polar' world	1,250,487,000	396,592,300	56,656,000	4.1	184	2.1	16
modern	1,302,484,000	367,477,400	37771000	3.6	175	2.2	8

Supplementary Table 1: Global summary statistics for each idealized continental configuration under default environmental conditions (i.e., pre-industrial $p\text{CO}_2$, modern $p\text{O}_2$, and modern sinking rate), including the modern cGENIE configuration for comparison. Ocean volume and areas are reported to seven significant figures; global mean ocean temperature and PO_4 to two significant figures; and global mean ocean O_2 and total POC export as integers.

Term	Coefficient	StdError	t Statistic	pvalue
(Intercept)	34.45	6.33	5.44	0
world_meridional	-22.72	6.41	-3.54	0
world_polar	-10.35	6.41	-1.61	0.11
pO2	-41.34	8.81	-4.7	0
sink	96.34	8.13	11.85	0
logpCO2	10.52	2.36	4.45	0
world_meridional :	24.06	7.07	3.4	0
pO2				
world_polar : pO2	-16.15	7.07	-2.28	0.02
world_meridional :	-2.84	6.84	-0.42	0.68
sink				
world_polar : sink	-6.75	6.84	-0.99	0.32
pO2 : sink	-50.82	10.21	-4.98	0
world_meridional :	-2.53	1.73	-1.46	0.14
logpCO2				
world_polar :	3.45	1.73	1.99	0.05
logpCO2				
pO2 : logpCO2	-7.64	2.58	-2.96	0
sink : logpCO2	-11.04	2.5	-4.42	0

Supplementary Table 2: Regression coefficients for the linear model used in the variance decomposition analysis. Coefficients are reported with standard errors, t-statistics, and p-values. Interaction terms represent pairwise combinations of predictors.

188

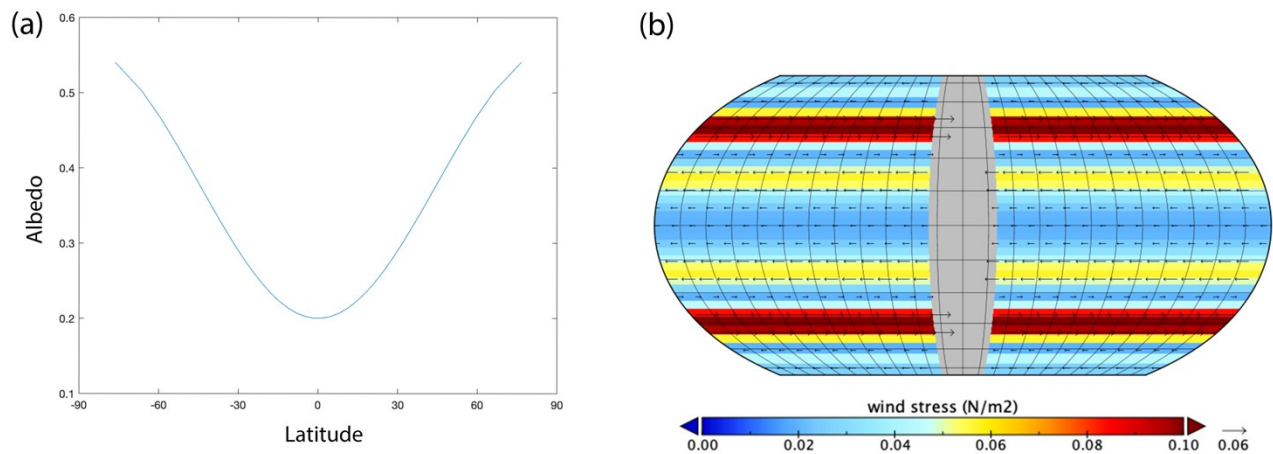
Term	Parameter importance (% variance explained)
pO_2	60.1
Sinking rate	24.6
World	7.7
$\log_2(pCO_2)$	0.01
World : pO_2	2.5
pO_2 : Sinking rate	1.9
Sinking rate : $\log_2(pCO_2)$	1.5
World : $\log_2(pCO_2)$	0.9
pO_2 : $\log_2(pCO_2)$	0.7
World : Sinking rate	0.1

189 **Supplementary Table 3:** Parameter importance of direct and interacting affects for the global
190 linear model–based variance decomposition described in S2.
191

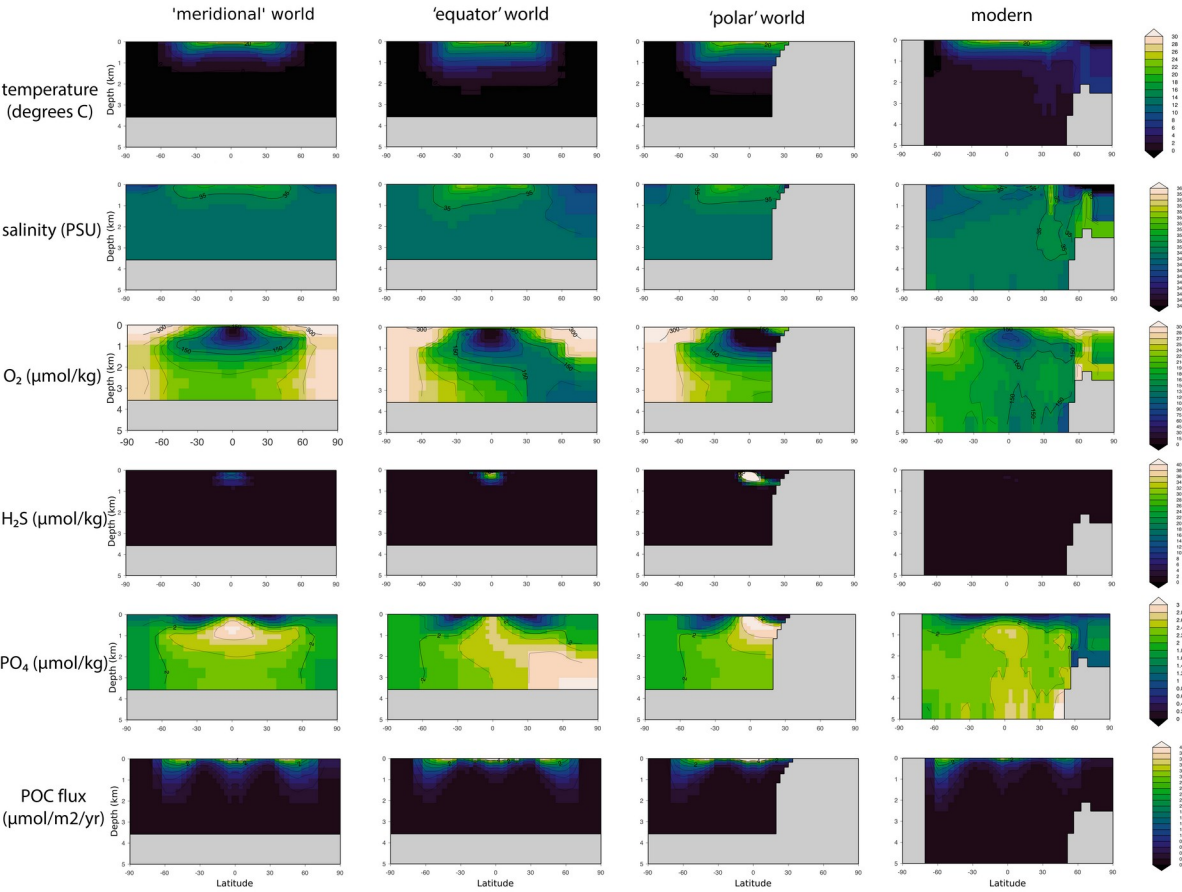
	pO₂ (times present PAL)					
World	0.2	0.3	0.4	0.5	0.8	1.0
Meridional	18.1	19.9	18.6	18.6	12.6	7.1
Equator	13.1	23.9	28.7	24.1	10.5	3.6
Polar	15.1	30.9	31.9	29.1	16.4	7.7

192 **Supplementary Table 4:** Standard deviations of the simulated anoxic shelf fraction (%) as a
 193 function of atmospheric pO₂ (expressed as fraction of present atmospheric level, PAL) for each
 194 continental configuration (meridional, equatorial, and polar). Values quantify the variability in
 195 benthic anoxia across all combinations of pCO₂ and organic matter sinking rate at a given pO₂
 196 level. Variability is highest at intermediate pO₂ levels and decreases toward higher oxygenation
 197 states, indicating reduced sensitivity of benthic anoxia to environmental perturbations under
 198 well-oxygenated conditions.

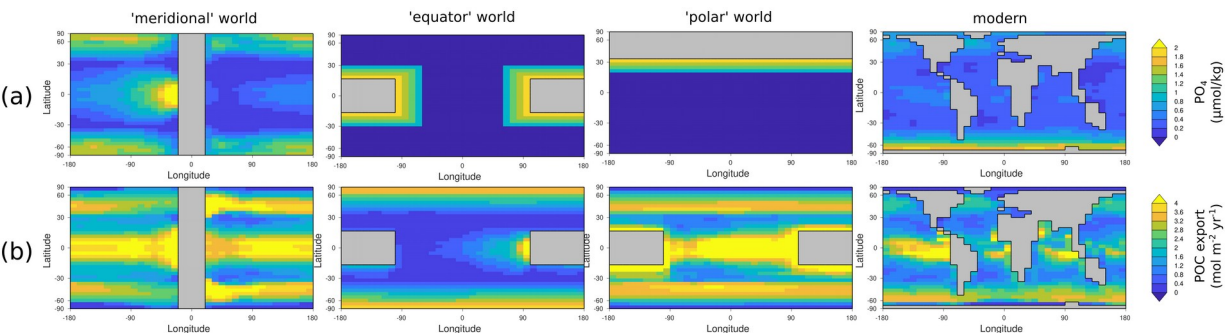
Supplementary Figures



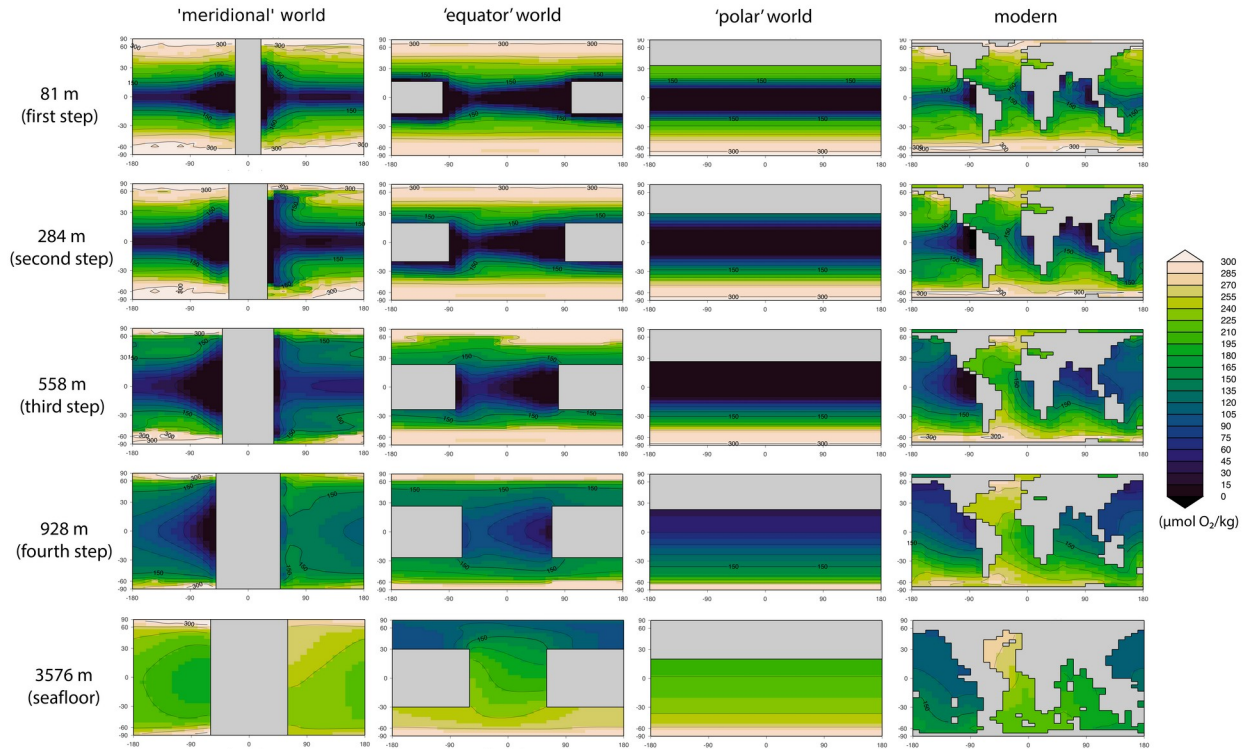
Supplementary Figure 1: Prescribed albedo profile and wind stress field for all idealized model worlds. (a) Latitude on the x-axis and albedo on the y-axis. (b) The intermediate zonal wind stress field as applied to a model world in the ‘meridional’ continental configuration, with arrows indicating direction and colors indicating magnitude. Vertical gridlines mark longitude in increments of 15° E-W, and horizontal gridlines mark latitude in increments of 15° N-S.



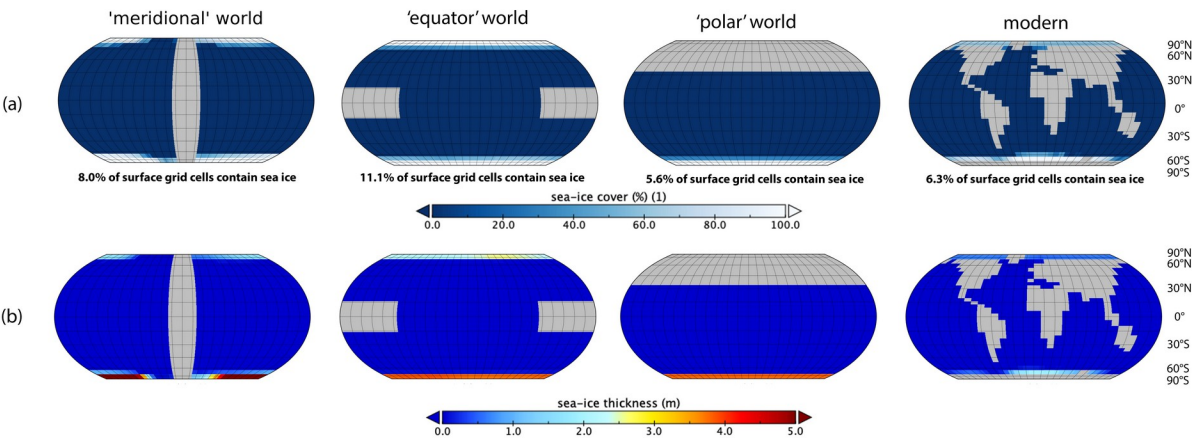
209 **Supplementary Figure 2: Zonal mean global ocean profiles** of temperature, salinity, O₂, H₂S,
210 PO₄, and POC flux for each idealized continental configuration under default environmental
211 conditions, including the modern configuration for comparison. Profiles are shown as latitude–
212 depth sections.



213 **Supplementary Figure 3: Surface ocean PO_4 concentration and particulate organic carbon**
214 **(POC) export flux** for each idealized continental configuration under default environmental
215 conditions and the modern configuration for comparison.

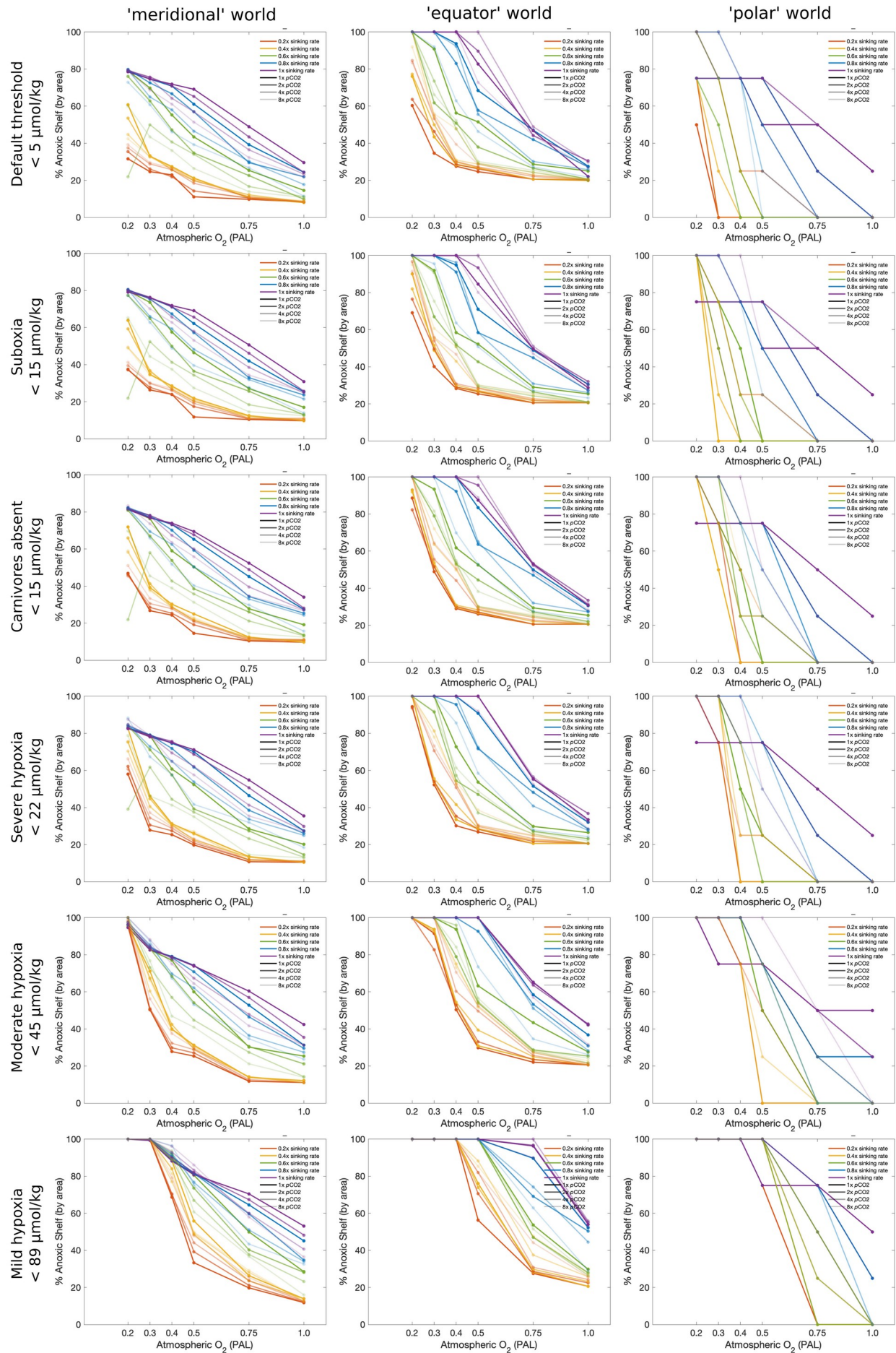


Supplementary Figure 4: Horizontal extent of the oxygen minimum zone (OMZ) relative to continental shelf geometry for each idealized continental configuration under default environmental conditions, including the modern configuration for comparison. Panels show horizontal slices (longitude on the x-axis, latitude on the y-axis) at the depths corresponding to successive shelf steps (81 m, 284 m, 558 m, 928 m) and the deep ocean seafloor (3576 m). Colors indicate dissolved oxygen concentration ($\mu\text{mol O}_2/\text{kg}^{-1}$), with darker shades (indigo to black) representing low-oxygen conditions and the core of the OMZ.

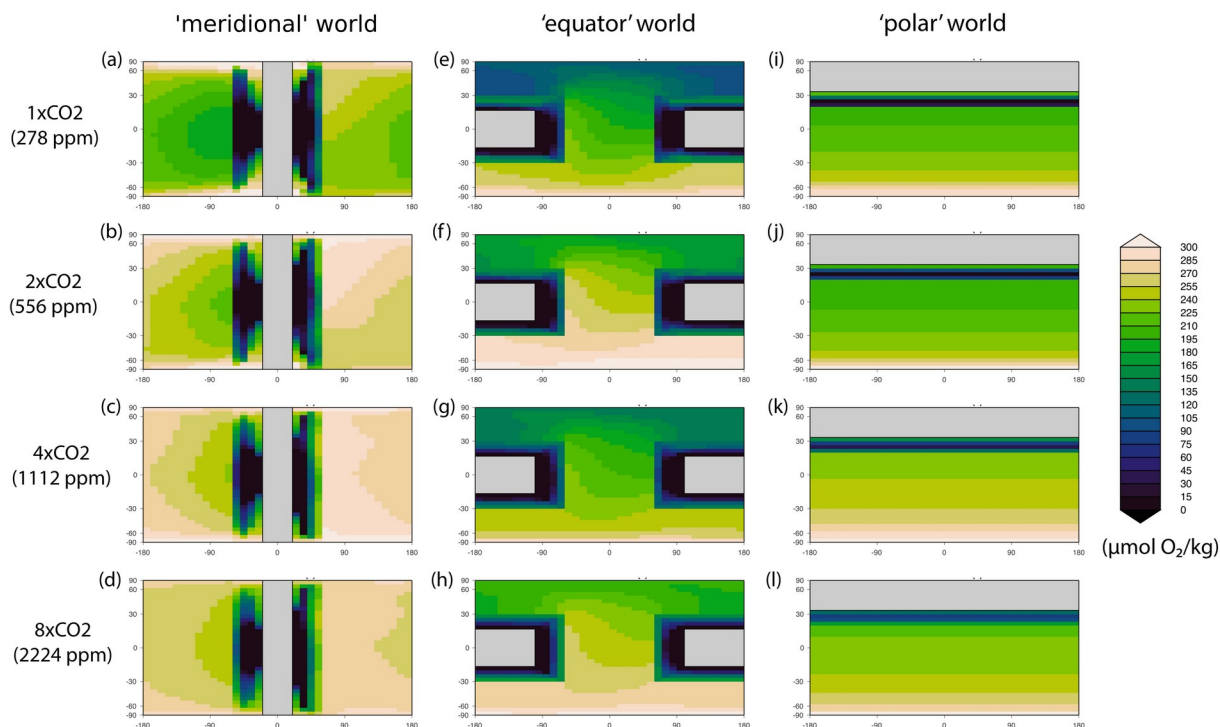


Supplementary Figure 5: Sea ice coverage and thickness for each idealized continental configuration under default environmental conditions, including the modern configuration for comparison. Vertical gridlines mark longitude at 15° intervals (E–W), and horizontal gridlines mark latitude at 15° intervals (N–S).

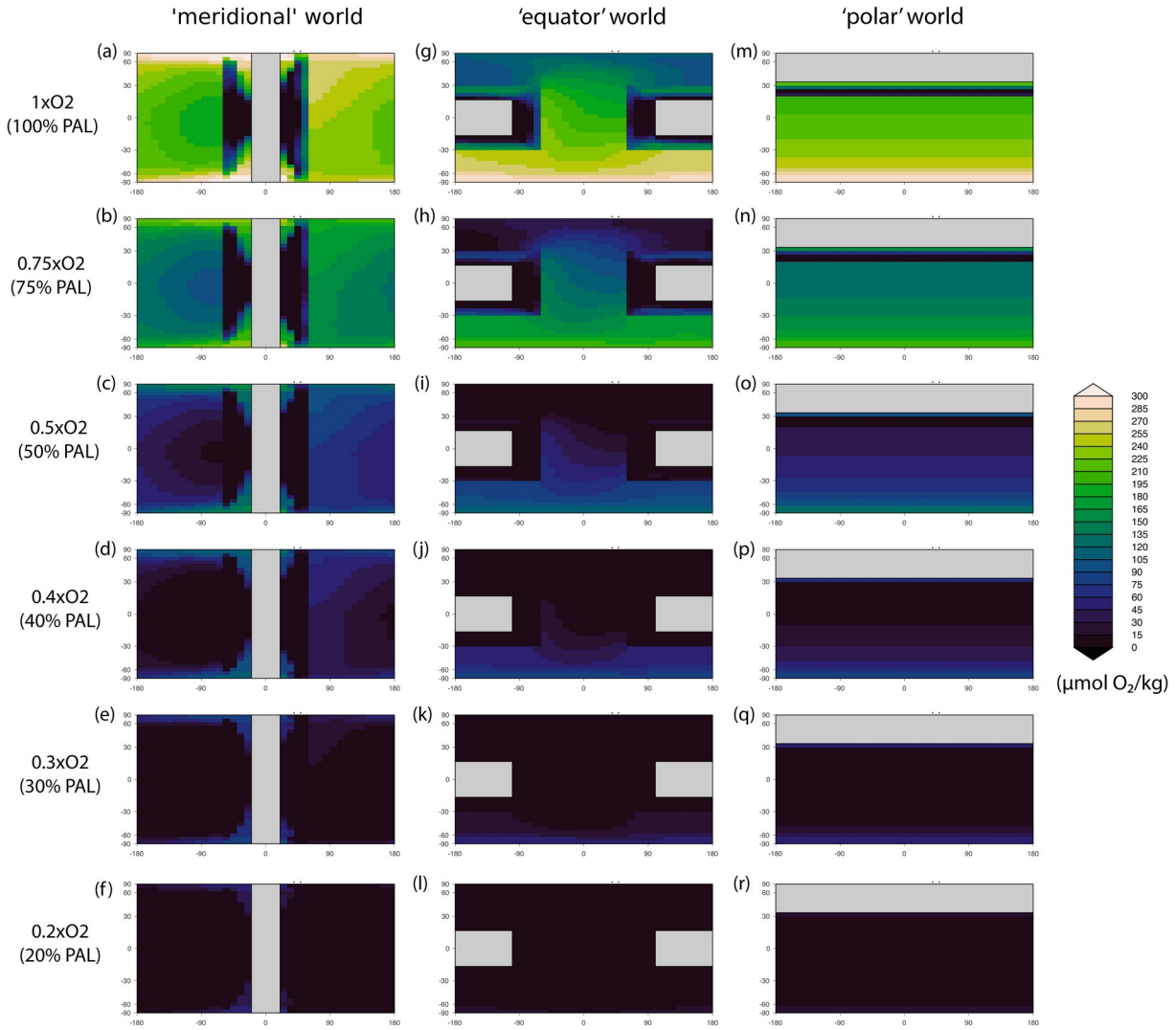
227



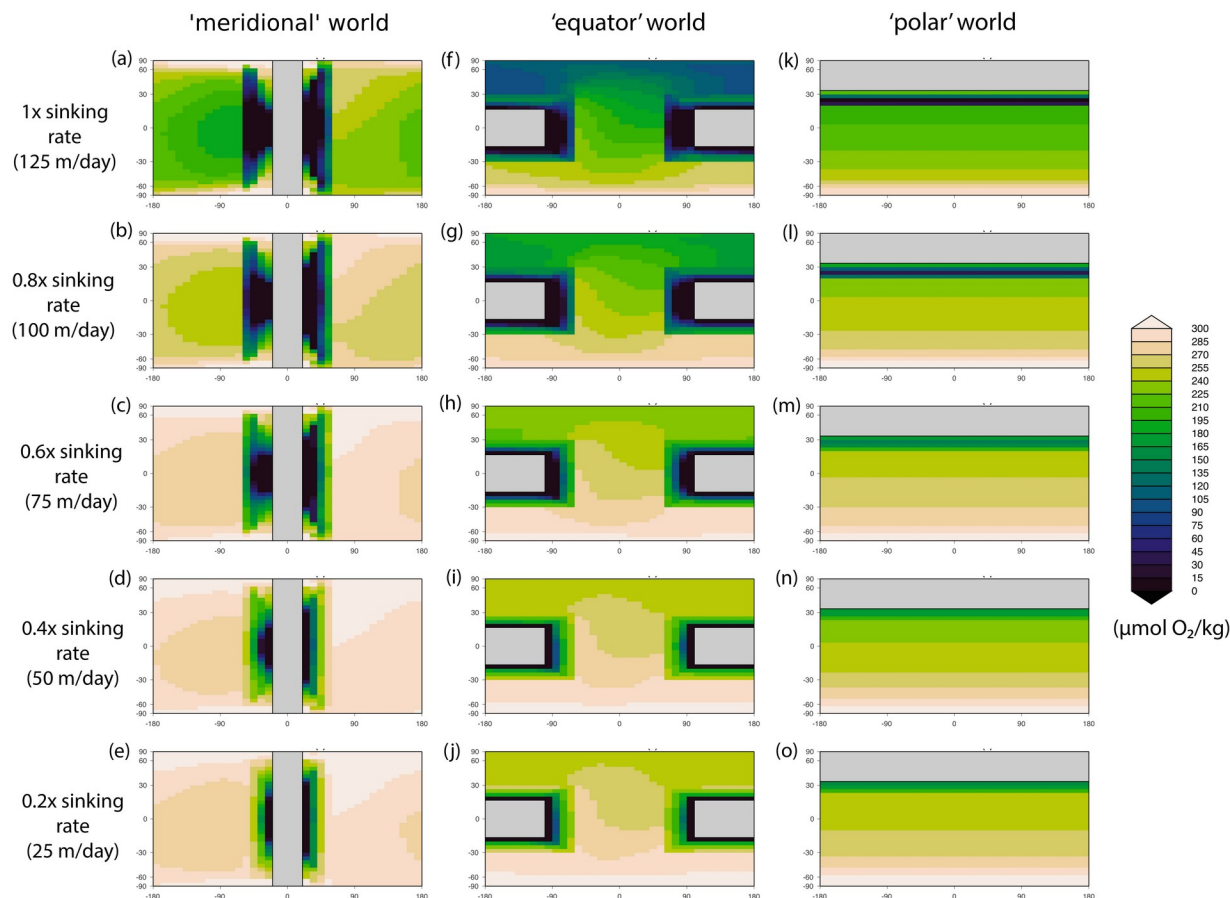
228 **Supplementary Figure 6: Sensitivity of the fraction of anoxic benthic shelf area (as shown**
229 **in Fig. 3) to different oxygen thresholds used to define anoxia.** Alternative thresholds are
230 based on Sperling et al. (2013). All other aspects of the analysis are identical to Fig. 3.



Supplementary Figure 7: Effect of atmospheric $p\text{CO}_2$ on benthic O_2 concentrations in each idealized continental configuration. Panels show seafloor O_2 concentrations ($\mu\text{mol O}_2 \text{ kg}^{-1}$) for increasing $p\text{CO}_2$ levels (1×, 2×, 4×, and 8× pre-industrial $p\text{CO}_2$; 278–2224 ppm), under constant atmospheric $p\text{O}_2$ (1× PAL) and sinking rate (1×; 125 m day⁻¹). Dark colors (indigo to black) indicate low-oxygen conditions.



236 **Supplementary Figure 8: Effect of atmospheric pO_2 on benthic O₂ concentrations in each**
 237 **idealized continental configuration.** Panels show seafloor O₂ concentrations ($\mu\text{mol O}_2 \text{ kg}^{-1}$)
 238 for decreasing pO_2 levels ($1\times$ to $0.2\times$ present atmospheric levels, PAL), under constant
 239 atmospheric pCO_2 ($1 \times$ pre-industrial pCO_2) and sinking rate ($1\times$; 125 m day^{-1}). Dark colors
 240 (indigo to black) indicate low-oxygen conditions.



Supplementary Figure 9: Effect of sinking rate on benthic O_2 concentrations in each idealized continental configuration. Panels show seafloor O_2 concentrations ($\mu\text{mol } O_2 \text{ kg}^{-1}$) for decreasing sinking rate ($1\times$ to $0.2\times$ default rate), under constant atmospheric $p\text{CO}_2$ ($1\times$ pre-industrial $p\text{CO}_2$) and $p\text{O}_2$ ($1\times$ PAL). Dark colors (indigo to black) indicate low-oxygen conditions.

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