A largely invariant marine dissolved organic carbon reservoir across Earth's history

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Marine dissolved organic carbon (DOC), the largest pool of reduced carbon in the oceans, plays an important role in the global carbon cycle and contributes to the regulation of atmospheric oxygen and carbon dioxide abundances. Despite its importance in global biogeochemical cycles, the long-term history of the marine DOC reservoir is poorly constrained. Nonetheless, significant changes to the size of the oceanic DOC reservoir through Earth's history have been commonly invoked to explain changes to ocean chemistry, carbon cycling, and marine ecology. Here, we present a revised view of the evolution of marine DOC concentrations using a mechanistic carbon cycle model that can reproduce DOC concentrations in both oxic and anoxic modern environments. We use this model to demonstrate that the overall size of the marine DOC reservoir has likely undergone very little variation through Earth's history, despite major changes in the redox state of the ocean–atmosphere system and the nature and efficiency of the biological carbon pump. A relatively static marine DOC reservoir across Earth's history renders it unlikely that major changes in marine DOC concentrations have been responsible for driving massive repartitioning of surface carbon or the large carbon isotope excursions observed in Earth's stratigraphic record and casts doubt on previously hypothesized links between marine DOC levels and the emergence and radiation of early animals.

marine carbon cycle | dissolved organic carbon | Precambrian | Ediacara biota

At ~600 petagrams of carbon (PgC = 10^{15} gC), dissolved organic carbon (DOC) is the largest pool of reduced carbon in the modern oceans, holding more than 200 times the carbon inventory of living marine biomass (1–3). Marine DOC exists along a continuum of reactivities and contains a range of labile and more refractory constituents (1–5). Because changes in the size or reactivity of each of these constituent pools can dramatically change both overall carbon storage in the oceans and the partitioning of carbon among surface reservoirs, the dynamics of marine DOC can potentially have major consequences for marine ecology and, on longer (geologic) time scales, atmospheric O_2 and CO_2 levels (2, 6, 7). Current views on the geologic history of the marine DOC pool and its links to major chemical and biological events (e.g., ocean–atmosphere oxygenation, the rise of eukaryotes, and marine mass extinctions) through Earth's history vary substantially. However, a common view is that the size of the DOC reservoir has undergone substantial changes and has played a key role in driving extreme global biogeochemical perturbations (e.g., refs. 7–10).

The marine DOC pool has been proposed to have been significantly larger than that of the modern oceans for the majority of Earth's history (11). A large marine DOC pool has been linked to the presence of a low-oxygen Earth state dominated by single-celled, prokaryotic life (12–14). An assumption underlying this view is that in an ocean in which both autotrophy and heterotrophy are dominated by prokaryotes, the transport of organic biomass into the deep ocean is attenuated by the slower sinking rate of smaller-sized prokaryotic cells. This in turn results in a much less efficient biological carbon pump, in which more of the biomass produced in the photic zone remains suspended in the surface ocean, reducing the fraction that reaches the ocean interior and seafloor. Such conditions, it has been argued, would promote the accumulation of a large marine DOC pool, which would act as a buffer against the accumulation of oxygen in Earth's ocean–atmosphere system (12–14).

It has also been hypothesized that the rise of larger eukaryotic algae to ecological dominance during the Neoproterozoic Era (1,000 to 541 Ma) (15–18) led to a smaller marine DOC pool, allowing dissolved oxygen to penetrate more deeply into Earth's oceans (13). In addition, it has been suggested that the radiation of zooplankton in the late Neoproterozoic Era or early Cambrian Period (e.g., 635 to 509 Ma) would have further modulated the structure of the biological carbon pump by packaging organic carbon in rapidly sinking fecal pellets produced by zooplankton (8, 19). In theory, zooplankton-assisted increases in organic matter burial could, by decreasing degradation of particulate organic matter (POC) to DOC in the ocean interior, have led to an even smaller DOC reservoir with even shorter residence times (8, 12, 13). This restructuring of marine carbon reservoirs has also been suggested to have catalyzed increases in marine oxygen levels and to have fostered the rise of multicellular organisms with greater oxygen requirements (11, 12).

In addition, anomalously large negative carbon isotope excursions recorded in Neoproterozoic strata, such as the Ediacaran Shuram excursion, have been attributed to oxidation of a substantial DOC reservoir (e.g., refs. 11, 20, and 21)—by some estimates up to 30-fold larger than the modern dissolved inorganic carbon (DIC) reservoir (10). It has also been suggested that changes in the DOC reservoir may have shaped Neoproterozoic climate and glacial dynamics (22). Furthermore, a large DOC reservoir is purported to have shaped the ecology of

Significance

Dissolved organic carbon (DOC) is the largest pool of reduced carbon in Earth's oceans, and changes in the size of this carbon reservoir can substantially impact atmospheric oxygen and carbon dioxide levels. It is widely believed that the marine DOC pool was large for most of Earth's history, buffering the ocean–atmosphere system against oxygenation and allowing for very large perturbations to Earth's carbon cycle. A new mechanistic model of oceanic DOC cycling suggests no substantial change in the size of the marine DOC pool throughout Earth's history. These results cast new light on the potential role of marine DOC in modulating Earth's ocean and atmosphere composition and in the evolution of the earliest complex life.

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some of the earliest complex ecosystems, such as rangeomorph-dominated communities of the Avalon Assemblage of the Ediacara Biota (e.g., refs. 23–26). Some workers have also suggested that the emergence of more complex animal behaviors, including new modes of heterotrophy by epibenthic organisms, as well as bioturbation, may have mediated contractions in the size of the marine DOC pool (e.g., refs. 27 and 28) and that fluctuations in the size of the marine DOC reservoir—whether biologically or environmentally mediated—may, in turn, have been responsible for extinction and taxonomic turnover between different Assemblages of the Ediacara Biota (29). Although previous empirical and modeling studies have invoked a large ancient DOC reservoir to explain observations from Earth's rock record (e.g., refs. 9 and 11), the underlying premise of dramatic changes to the size of oceanic DOC reservoir has yet to be explicitly evaluated in a quantitative and mechanistic framework.

A Mechanistic Model for Marine DOC Cycling

To delineate how the marine DOC pool has changed through time, we have developed a mechanistic model of global marine DOC cycling. The core of the model is a previously developed particle-based representation of the marine biological pump (30), which is coupled to a parameterization of DOC dynamics embedded into a simple ocean model designed to capture the large-scale effects of global, density-driven circulation on the marine DOC cycle (Fig. 1). The oceanic regions in the model include continental shelf, surface, intermediate, deep, downwelling high-latitude, upwelling high-latitude, upwelling slope, and upwelling surface ocean environments (Fig. 1). The model explicitly tracks the production, consumption, and transfer of DOC and dynamically calculates its abundance throughout the ocean (Fig. 1).

The particle model couples stochastic particle aggregation and transport with temperature- and oxygen-dependent organic matter remineralization. Aggregates, the constitutive elements of the model, are clusters of planktonic cells (e.g., diatoms, non-skeletal algae, picoplankton, zooplankton) and terrigenous dust particles. In the uppermost layer of the ocean, we stochastically "seed" a stock of primary particles based on assumed primary productivity of picoplanktonic and algal biomass, algal carbonate flux, and surface dust flux (30). These particles then sink from the surface ocean and interact in the ocean interior through aggregation/disaggregation and organic matter breakdown.

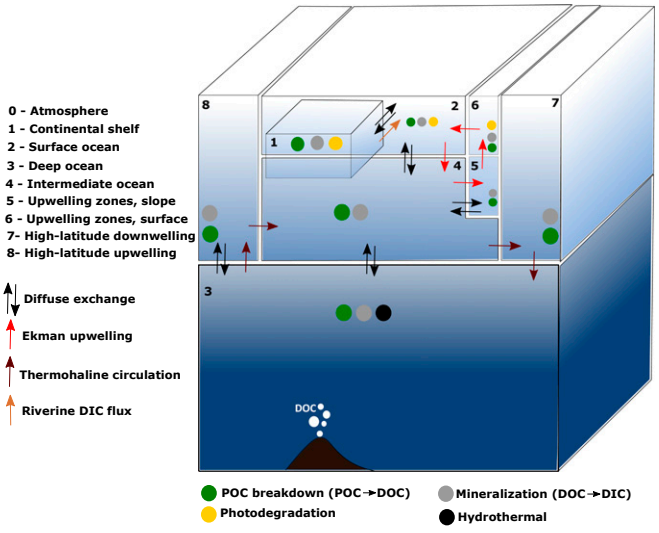

Fig. 1. Schematic representation of the ocean–atmosphere box model for DOC. DOC concentrations in each oceanic box are controlled by physical transport mechanisms, carbon degradation (POC to DOC transformation), mineralization (DOC to DIC), hydrothermal flux, and photodegradation in the photic zone.

As oceanic aggregates sink through the water column, POC with high molecular weights (>>1,000 Dalton) is degraded and depolymerized into smaller organic molecules with lower molecular weights (e.g., DOC) (31). The resultant DOC is then further degraded and remineralized, which results in the formation of DIC (31). The overall rate of carbon transformation from POC to DIC is thus controlled by the rates of DOC production from POC and DIC production from DOC. Many of the mechanisms controlling the rate of this multistage conversion of organic matter to inorganic carbon are not fully understood. However, we use a well-established, empirically based power-law framework for organic matter degradation that has been modified to account for the effects of oxygen and seawater temperature on the overall rate of POC degradation (*SI Appendix*) (32, 33). The rate of the terminal oxidation step, in which DOC is converted to DIC, is based on a Monod model that includes a half-saturation for DOC uptake by heterotrophs and a maximum rate of DOC degradation (34, 35). Specifically, there is now compelling evidence that DOC degradation is regulated by the concentration of intrinsically labile compound classes and the metabolic costs associated with their degradation (34, 35) (*SI Appendix*).

Critically, our model can accurately reproduce measured DOC concentrations across a wide range of modern environments (Fig. 2). Foremost, the model reproduces depth-dependent DOC abundance in all major regions of the oceans using constraints on modern rates of primary productivity, ocean and hydrothermal circulation, and temperature. With empirically constrained temperatures, physical dynamics, and primary productivities (but the same parameterization scheme as for carbon cycling; reference *SI Appendix*), the model also reproduces the dynamics of DOC recycling in modern anoxic systems, including the Black Sea (the largest modern marine anoxic and sulfidic basin) and Lac Pavin (a well-studied anoxic and iron-rich lake). The close correspondence between our model results and empirical data indicates that our model captures the major processes regulating DOC production, accumulation, and recycling across a wide range of marine and lacustrine environments of varying redox states. Full model details, documentation of model assumptions, and information on error propagation are provided in *SI Appendix*.

Factors Regulating Marine DOC Concentrations through Earth's History

Having demonstrated that our model can capture key processes regulating modern DOC cycling, we next quantified changes in the marine DOC reservoir in three different scenarios that represent endmembers in Earth's evolving ocean–atmosphere redox state, along with major changes in the structure and efficiency of the marine biological carbon pump. The first two scenarios correspond broadly to the Precambrian oceans (>541 Mya), in which marine primary production is commonly interpreted to have been dominated by single-celled cyanobacteria, and surface marine oxygen levels were likely between 0.1 and 10% of those in the modern surface oceans (36). The third scenario represents a condition that broadly mimics the modern Earth system, in which the marine biological pump is more ecologically complex and includes eukaryotic algae, fecal pellet–producing zooplankton, and zooplankton practicing diel vertical migration. Finally, to account for the intrinsic uncertainty in values of a number of model parameters, we employ a stochastic approach wherein potential values for these input parameters were randomly sampled across a wide range (assuming uniform priors; *SI Appendix*, Table S1), and the model is spun up to steady state to estimate ocean DOC distributions for each case.

Our model suggests that the size of the oceanic DOC reservoir has been relatively constant throughout Earth's history (Figs. 3 and 4). Specifically, in all scenarios and regardless of changes in

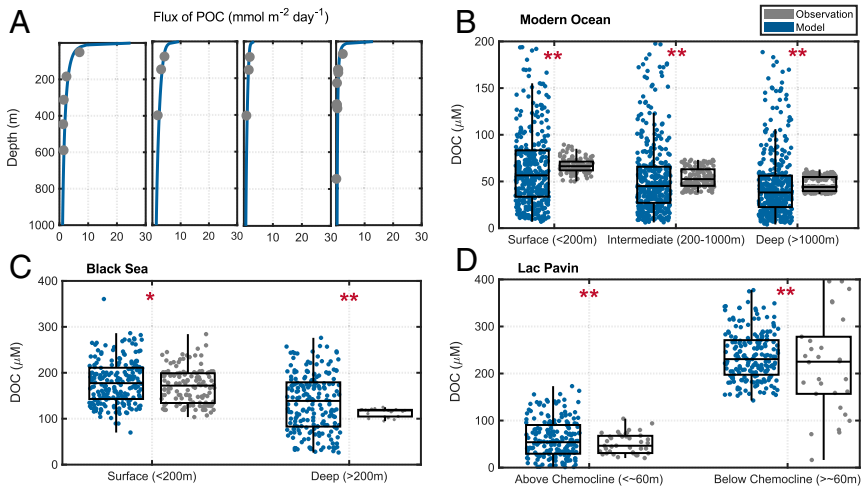

Fig. 2. Results of calibrating the particle-tracking model of the marine biological pump to observed POC fluxes in four different sites in the North Atlantic (61) (*A*) and from the box model for the modern oceans (*B*), the anoxic and sulfide-rich Black Sea (*C*), and the anoxic and iron-rich Lac Pavin (*D*). POC fluxes from the particle-tracking model (*A*) are obtained by calculating the concentration of POC at each depth using a power law for organic matter degradation. The reactivity of organic matter used in the power law is calculated from a depth profile of POC age obtained by considering the average settling rate of aggregates in the particle-tracking model and their corresponding depths (*SI Appendix*). The observed POC fluxes are derived from a series of different sites across the North Atlantic (61). The DOC concentration in different modern settings, including the modern ocean, the Black Sea, and Lac Pavin, is calculated by considering the same set of assumptions for production and consumption of DOC and using distinct physical transport coefficients for each of these settings (62–66). Symbols "*" and "**" denote results of *t* tests performed to assess whether differences between model results and modern observations are significantly different; * denotes a *P* value > 0.05, indicating that the null hypothesis of no significant difference cannot be rejected; ** denotes a *P* value > 0.1.

atmospheric oxygen abundance or the structure and efficiency of the biological pump caused by increasing ecological complexity in the surface ocean, DOC concentrations in all oceanic regions represented in the model remained well below 300 μM, with the most likely range for all regions (>95% of results) being less than 100 μM DOC, very similar to that of the modern oceans (Fig. 3). In both our model and in modern systems (see ref. 37), increases in oxygen availability lead to enhanced rates of DOC oxidation. However, this effect is largely balanced by an increase in the generation of DOC from the degradation of POC, resulting in a relatively constant DOC reservoir. This is consistent with evidence from modern oxic sediments in which an increased rate of POC degradation under oxic conditions leads to lower POC concentrations and lower burial efficiency (e.g., ref. 33). Unlike oxygen, the availability of electron acceptors under anoxic conditions (e.g., sulfate, metal oxides) does not appear to have any impact on rates of DOC oxidation and DIC production (37, 38). This is in accordance with observations from modern anoxic sediments in which rates of organic matter degradation have been found to be largely invariant through the transition from the sulfate-reducing zone to the methanic zone, suggesting that terminal electron acceptors exert minimal control over upstream hydrolytic and fermentative processes (e.g., ref. 38).

Our results also indicate that the rise of eukaryote-dominated ecosystems in the oceans would have had a minimal influence on the size of the marine DOC reservoir. In particular, a shift from a biological pump dominated by slow-sinking, single-celled organisms to one that is dominated by eukaryotic algae and that contains zooplankton with the ability to vertically migrate and produce dense, rapidly sinking fecal pellets has a minimal overall impact on oceanic DOC abundance. This is in marked contrast to previous hypotheses that the rise of eukaryotic algae would have significantly impacted the efficiency of the biological pump and marine DOC concentrations (e.g., refs. 8, 10, and 14). This apparent discrepancy stems in part from observations and model results suggesting that all sinking organic matter in marine systems will become a part of a complex aggregation–disaggregation system of marine particles, rather than sinking as single, isolated cells as has been envisioned by previous models—regardless of whether algae or fecal pellet–producing zooplankton are prevalent in these systems (39). For instance, experimental studies indicate substantial aggregation of particles in the absence of zooplankton, with an important role for mineral ballasting in regulating particle aggregation and increasing the settling velocity of aggregates (e.g., refs. 39 and 40).

Changes to seawater surface temperature emerge in our model as the single strongest lever on the concentration of marine DOC. Specifically, our modeling results indicate that a cooling climate would act to promote the accumulation of a significantly larger DOC pool, whereas warming would lead to a smaller DOC reservoir (30, 41, 42). By suppressing rates of DOC consumption by heterotrophs, global cooling elevates the mean marine DOC concentration by up to several hundred μM in our model (Fig. 4). In this light, Late Cenozoic oceans (including today's oceans) may actually have some of the highest DOC concentrations in all of Earth's history. Additionally, severe cooling events such as those that occurred during Neoproterozoic low-latitude "Snowball Earth" glaciations could have potentially led to the accumulation of DOC to several hundreds of μM, about three times higher than typical DOC concentrations in the modern oceans (<100 μM), assuming roughly modern levels of primary productivity. Nonetheless, even in extreme events—such as during Snowball Earth glacial episodes—our model suggests DOC concentrations would have been many orders of magnitude lower than previously hypothesized (9, 11).

Impact of the Marine DOC Reservoir on Geochemical and Paleontological Records

Our model results suggest that the marine DOC reservoir would likely have had only a minimal impact on the isotopic composition of marine DIC, thus indicating that marine DOC is unlikely to have played a significant role in driving global carbon isotope excursions (cf. refs. 9 and 11). For instance, estimates derived from non–steady-state marine carbon cycle models have been used to suggest that oceanic DOC concentrations at least 10 times larger than the marine DIC pool were needed to drive prominent Neoproterozoic negative carbon isotope excursions, such as the Shuram excursion (e.g., refs. 9 and 11). Conservatively assuming a modern value for the marine DIC reservoir, this would translate into roughly 400,000 PgC in the marine DOC pool, more than

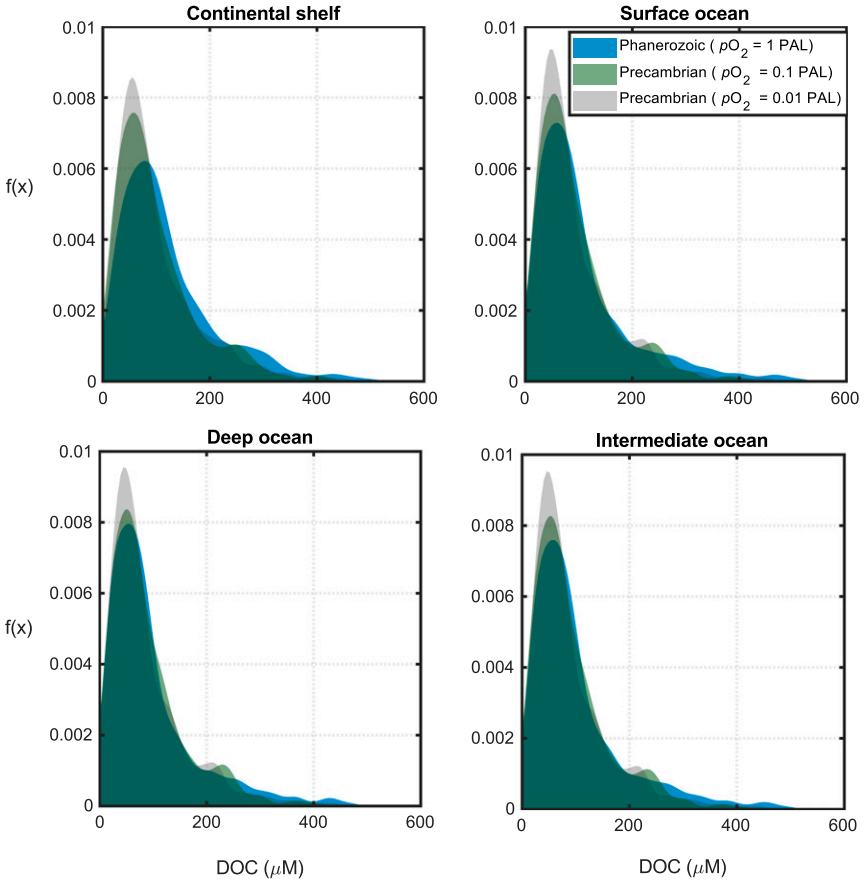

Fig. 3. Statistical distributions of modeled steady-state marine DOC abundance in four major ocean regions for the three idealized Earth system scenarios discussed in the text. In the Precambrian scenarios, the marine biological pump is dominated by single-celled bacterial primary producers, and atmospheric oxygen levels (pO_2) are assumed to be less than modern. We considered two end-member pO_2 levels of 0.01 and 0.1 times the present atmospheric level (PAL) for the Precambrian simulations. The Phanerozoic scenario represents a modern-like condition in which there is a wide range of eukaryotic algae in the oceans, as well as zooplankton with the capability of vertical migration and production of large, rapidly sinking fecal pellets.

500 times larger than that of the modern oceans (cf. ref. 43). Our results thus strongly support suggestions that prominent negative carbon isotope excursions during late Precambrian time are more plausibly tied either to oxidation of geologic carbon reservoirs (e.g., ref. 44) or to diagenetic alteration (45, 46), rather than the oxidation of a large DOC reservoir (9, 11).

Evidence for a relatively invariant marine DOC reservoir through Earth's history also provides critical insights into the environmental backdrop for the Neoproterozoic emergence of animals. It has commonly been proposed, largely on the basis of molecular clock predictions (e.g., refs. 47 and 48), that animals emerged in the Tonian (1,000 to 720 Ma) or Cryogenian (720 to 635 Ma). However, the first widely accepted body and trace fossil evidence for complex and macroscopic multicellular heterotrophs, including bilaterian animals, appears much later, during the Ediacaran Period (e.g., ref. 49). The phylogenic affinities of many Ediacaran fossils, foremost the enigmatic Ediacara Biota, remain poorly constrained, with proposed affinities ranging from sponges to placozoans, giant protists, lichens, or even an extinct kingdom (50–52)—but they are commonly inferred to consist largely of stem- or even crown-group animals (e.g., refs. 50, 53, and 54). Although Ediacara communities comprising the younger White Sea and Nama Assemblages flourished in shallow marine environments, communities of the older Avalon Assemblage, dominated by rangeomorphs (benthic frondose organisms with fractal morphologies; e.g., ref. 55), appear to have been restricted to deep marine environments (56, 57). Rangeomorphs, as well as potentially sponge-grade organisms such as *Thectardis* (28), have commonly been proposed to have fed via osmotrophy (i.e., osmotic uptake of dissolved organic nutrients), presumably sustained by a massive reservoir of labile DOC (23, 25, 26, 58). Our model results—indicating that DOC abundance in late Ediacaran oceans is unlikely to have been substantially higher than that of the modern oceans—call into question this longstanding interpretation of the paleoecology of Earth's earliest animal ecosystems.

Neoproterozoic oceans with a DOC inventory similar to that of the modern oceans, as suggested by our work, would have provided a distinctively different environment for the initial radiation of complex animal life than oceans characterized by a vast DOC reservoir. More broadly, these results suggest that previous inferences regarding the role played by particular environmental factors in the ecology of early animals should be revisited. It is unlikely that decreasing marine DOC levels would have played a role in the decline and extinction of Ediacara taxa, as has previously been suggested (e.g., ref. 29). Additionally, our modeling results may help resolve a longstanding contradiction between geochemical models and ecological predictions regarding the rise of multicellular heterotrophs. Previous geochemical modeling work has led to the inference that heterotrophic multicellularity (i.e., animals and fungi) emerged against a backdrop of a vast DOC reservoir (e.g., refs. 9 and 10). However, under a high-DOC scenario, metabolizable organic matter would have been nonlimiting, as DOC levels would have been orders of magnitude higher than dissolved oxygen levels. Therefore, many of the commonly assumed benefits

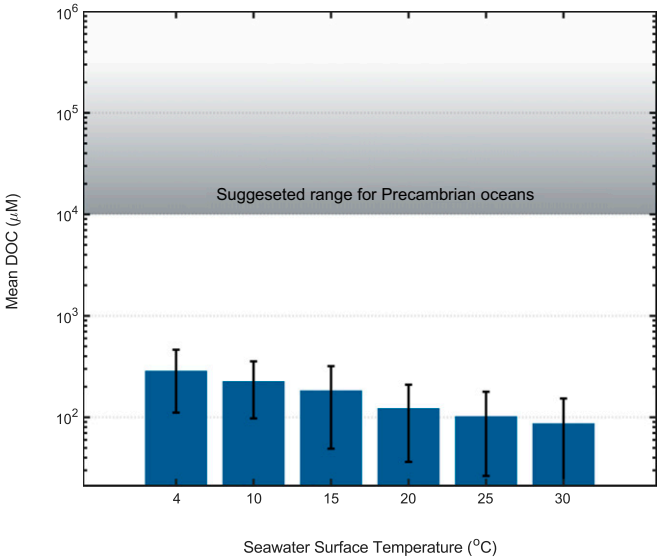

Fig. 4. Effect of seawater surface temperature on marine DOC concentrations. Each value represents the average DOC concentration (and associated error [±1σ] for the stochastic simulation) in the surface ocean (Box 1 in Fig. 1). By lowering rates of heterotrophic DOC degradation, a decrease in seawater surface temperature results in an increase in the size of the surface ocean DOC reservoir. The shaded box corresponds to suggestions from previous work for the range of DOC in Precambrian oceans (>541 Mya) (9, 11).

of complex multicellularity and key features of basal metazoan clades—particularly those that facilitate enhanced delivery of organic substrates (e.g., cnidocysts in cnidarians)—would not, by this logic, have had significant energetic benefits or obvious evolutionary advantage over strategies employed by single-celled organisms. In contrast, a largely static marine DOC reservoir offers a simple path toward resolving these contradictory views. The body plans of Neoproterozoic animals may, in contrast to previous conceptual models (e.g., refs. 24–26), have evolved to facilitate more efficient uptake of metabolizable organic matter in relatively DOC-lean environments.

Conclusions

A mechanistic model of the marine biological carbon pump and large-scale DOC cycling suggests that the marine DOC reservoir has remained relatively constant through much of Earth's history. Notably, regardless of the substantial changes that have occurred in the biological and chemical structure of the oceans through time, the concentration of marine DOC would have been dynamically buffered near its observed range in the modern oceans. Our results further indicate that while climate cooling can potentially enhance the concentration of marine DOC up to several hundreds of μM, even during extreme glacial episodes such as the Cryogenian Snowball Earth events inferred temperature declines would have been insufficient to explain the large carbon isotope excursions that characterize the upper Neoproterozoic stratigraphic record. Finally, our results do not corroborate previous interpretations, influenced in large part by inferences of an anomalously large marine DOC reservoir, that osmotrophy would have played a significant role in shaping the evolution of the earliest multicellular eukaryotes, reviving fundamental questions about the ecology and evolution of early complex life.

Materials and Methods

The Box Model. The concentration of DOC in each oceanic box is calculated by solving the following differential equation:

$$\frac{dDOC_i}{dt} = F_{POC-DOC} - F_{DOC-DIC} - F_{Photo} + F_{transport}, \quad [1]$$

where DOC_i is the concentration of DOC in box i. $F_{POC\text{-}DOC}$, $F_{DOC\text{-}DIC}$, F_{Photo} (only for surface boxes), and $F_{transport}$ correspond, respectively, to the fluxes of DOC production from POC, DOC transformation into DIC, photodegradation of DOC, and the sum of all the physical transport fluxes into and out of the box. The production flux of DOC from POC is calculated by multiplying the area of the box by the depth-integrated rate of POC breakdown resulting from the biological pump model. The rate of POC breakdown is modeled as a power-law function, following a previously established framework, which is modified to also account for the effects of oxygen and temperature (30, 33).

$$R_{POC-DOC} = Q_{10}^{\frac{T-T_{ref.}}{10}} (-bt^{-a}C), \quad [2]$$

where T is the ambient environmental temperature, T_{ref} is a reference temperature, and Q_{10} is the temperature dependency factor, which for most biological systems varies between 1.5 and 2.5 (59, 60). C is the concentration of organic matter as POC, and the constants a and b define the rate of organic carbon mineralization, which varies as a function of environmental oxygen availability (38). The rate of DOC to DIC production is considered to follow a Monod scheme, consistent with experimental and modeling studies in the modern oceans (e.g., ref. 34):

$$F_{DOC-DIC} = \alpha\, R_{POC-DOC} \frac{[DOC]}{k_{DOC} + [DOC]} A_i \quad [3]$$

As denoted in Eq. 3, $R_{POC\text{-}DOC}$ is the depth-integrated rate of conversion of POC to DOC, calculated using the power law described above and obtained by the biological carbon pump model; $[DOC]$ is the concentration of DOC in each oceanic box; k_{DOC} is the half-saturation constant for DOC degradation; A_i is the area of the corresponding oceanic box; and α is a fitting parameter obtained by fitting the DOC depth profile from our model to the measured depth profiles in the modern ocean. Mechanistically, the factor k_{DOC} represents the impact of the "dilution hypothesis" in which a low DOC concentration is invoked to explain large deep-ocean DOC storage (e.g., ref. 34). The value of k_{DOC} has been suggested to be ~231.16 ± 899.99 μM (*SI Appendix*, Table S1) (35).

The Biological Carbon Pump Model. At its core, the biological carbon pump is comprised of a particle model that couples stochastic particle aggregation and transport with temperature- and oxygen-dependent organic matter remineralization. Aggregates, the constitutive elements of the model, are clusters of phytoplankton cells (e.g., diatoms, nonskeletal algae, picoplankton, zooplankton) and terrigenous dust particles. In the uppermost layer of the ocean, we stochastically "seed" a stock of primary particles based on assumed primary productivity of picoplankton and algal biomass, algal calcite flux, and surface dust flux. These particles then sink from the surface ocean and interact in the ocean interior through aggregation/disaggregation and organic matter respiration. To account for spatial heterogeneity, the model calculates the sinking rates of a large number of aggregates (10^6) at each depth layer. Dividing the ocean into 1,000 depth intervals results in 10^9 potential aggregates. A full description of the model is provided in *SI Appendix* as well as in ref. 30.

Data Availability. All study data are included in the article and/or *SI Appendix*.

1. D. A. Hansell, C. A. Carlson, *Biogeochemistry of Marine Dissolved Organic Matter* (Elsevier Inc., ed. 2, 2014).
2. D. A. Hansell, Recalcitrant dissolved organic carbon fractions. *Annu. Rev. Mar. Sci.* **5**, 421–445 (2013).
3. D. J. Repeta, "Chemical characterization and cycling of dissolved organic matter" in *Biogeochemistry of Marine Dissolved Organic Matter*, D. A. Hansell, C. A. Carlson, Eds. (Elsevier, 2015), pp. 21–63.
4. T. Dittmar, "Reasons behind the long-term stability of dissolved organic matter" in *Biogeochemistry of Marine Dissolved Organic Matter*, D. A. Hansell, C. A. Carlson, Eds. (Elsevier Inc., ed. 2, 2015), pp. 369–388.
5. A. M. Kellerman, D. N. Kothawala, T. Dittmar, L. J. Tranvik, Persistence of dissolved organic matter in lakes related to its molecular characteristics. *Nat. Geosci.* **8**, 454–457 (2015).
6. F. Joos, G. K. Plattner, T. F. Stocker, Global warming and marine carbon cycle feedbacks on future atmospheric CO_2. *Science* **284**, 464–467 (1999).
7. D. H. Rothman, J. M. Hayes, R. E. Summons, Dynamics of the Neoproterozoic carbon cycle. *Proc. Natl. Acad. Sci. U.S.A.* **100**, 8124–8129 (2003).
8. T. M. Lenton, R. A. Boyle, S. W. Poulton, G. A. Shields-Zhou, N. J. Butterfield, Co-evolution of eukaryotes and ocean oxygenation in the Neoproterozoic era. *Nat. Geosci.* **7**, 257–265 (2014).

9. G. A. Shields *et al*., Unique Neoproterozoic carbon isotope excursions sustained by coupled evaporite dissolution and pyrite burial. *Nat. Geosci.* **12**, 823–827 (2019).
10. G. A. Shields, "Earth system transition during the Tonian–Cambrian interval of biological innovation: Nutrients, climate, oxygen and the marine organic carbon capacitor" in *Geological Society Special Publication*, A. T. Brasier, D. McIlroy, N. McLoughlin, Eds. (Geological Society of London, 2017), pp. 161–177.
11. D. H. Rothman, J. M. Hayes, R. E. Summons, *Dynamics of the Neoproterozoic Carbon Cycle* (National Academy of Sciences, 2003).
12. G. A. Logan, J. M. Hayes, G. B. Hieshima, R. E. Summons, Terminal Proterozoic reorganization of biogeochemical cycles. *Nature* **376**, 53–56 (1995).
13. N. J. Butterfield, Oxygen, animals and oceanic ventilation: An alternative view. *Geobiology* **7**, 1–7 (2009).
14. T. M. Lenton, S. J. Daines, The effects of marine eukaryote evolution on phosphorus, carbon and oxygen cycling across the Proterozoic-Phanerozoic transition. *Emerg. Top. Life Sci.* **2**, 267–278 (2018).
15. J. J. Brocks, *et al*., The rise of algae in Cryogenian oceans and the emergence of animals. *Nature* **548**, 578–581 (2017).
16. J. J. Brocks, The transition from a cyanobacterial to algal world and the emergence of animals. *Emerg. Top. Life Sci.* **2**, 181–190 (2018).
17. T. T. Isson *et al*., Tracking the rise of eukaryotes to ecological dominance with zinc isotopes. *Geobiology* **16**, 341–352 (2018).
18. J. A. Zumberge, D. Rocher, G. D. Love, Free and kerogen-bound biomarkers from late Tonian sedimentary rocks record abundant eukaryotes in mid-Neoproterozoic marine communities. *Geobiology* **18**, 326–347 (2020).
19. T. M. Lenton, S. J. Daines, The effects of marine eukaryote evolution on phosphorus, carbon and oxygen cycling across the Proterozoic-Phanerozoic transition. *Emerg. Top Life Sci.* **2**, 267–278 (2018).
20. D. A. Fike, J. P. Grotzinger, L. M. Pratt, R. E. Summons, Oxidation of the Ediacaran ocean. *Nature* **444**, 744–747 (2006).
21. C. Verdel, B. P. Wernicke, S. A. Bowring, The Shuram and subsequent Ediacaran carbon isotope excursions from southwest Laurentia, and implications for environmental stability during the metazoan radiation. *Geol. Soc. Am. Bull.* **123**, 1539–1559 (2011).
22. W. R. Peltier, Y. Liu, J. W. Crowley, Snowball Earth prevention by dissolved organic carbon remineralization. *Nature* **450**, 813–818 (2007).
23. S. A. F. Darroch, M. Laflamme, M. E. Clapham, Population structure of the oldest known macroscopic communities from Mistaken Point, Newfoundland. *Paleobiology* **39**, 591–608 (2013).
24. M. Laflamme, S. Xiao, M. Kowalewski, Osmotrophy in modular Ediacara organisms. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 14438–14443 (2009).
25. A. Seilacher, "Late Precambrian and early Cambrian Metazoa: Preservational or real extinctions?" in *Patterns of Change in Earth Evolution*, H. D. Holland, A. F. Trendall, Eds. (Springer, 1984), pp. 159–168.
26. E. A. Sperling, K. J. Peterson, M. Laflamme, Rangeomorphs, *Thectardis* (Porifera?) and dissolved organic carbon in the Ediacaran oceans. *Geobiology* **9**, 24–33 (2011).
27. R. A. Boyle, T. W. Dahl, C. J. Bjerrum, D. E. Canfield, Bioturbation and directionality in Earth's carbon isotope record across the Neoproterozoic-Cambrian transition. *Geobiology* **16**, 252–278 (2018).
28. E. A. Sperling, D. Pisani, K. J. Peterson, "Poriferan paraphyly and its implications for Precambrian palaeobiology" in *Geological Society Special Publication*, P. Vickers-Rich, P. Komarower, Eds. (Geological Society of London, 2007), pp. 355–368.
29. A. D. Muscente, T. H. Boag, N. Bykova, J. D. Schiffbauer, Environmental disturbance, resource availability, and biologic turnover at the dawn of animal life. *Earth Sci. Rev.* **177**, 248–264 (2018).
30. M. Fakhraee, N. J. Planavsky, C. T. Reinhard, The role of environmental factors in the long-term evolution of the marine biological pump. *Nat. Geosci.* **13**, 812–816 (2020).
31. D. J. Burdige, Preservation of organic matter in marine sediments: Controls, mechanisms, and an imbalance in sediment organic carbon budgets? *Chem. Rev.* **107**, 467–485 (2007).
32. J. J. Middelburg, A simple rate model for organic matter decomposition in marine sediments. *Geochim. Cosmochim. Acta* **53**, 1577–1581 (1989).
33. S. Katsev, S. A. Crowe, Organic carbon burial efficiencies in sediments: The power law of mineralization revisited. *Geology* **43**, 607–610 (2015).
34. J. M. Arrieta *et al*., Dilution limits dissolved organic carbon utilization in the deep ocean. *Science* **348**, 331–333 (2015).
35. J. D. Wilson, S. Arndt, Modeling radiocarbon constraints on the dilution of dissolved organic carbon in the deep ocean. *Global Biogeochem. Cycles* **31**, 775–786 (2017).
36. T. W. Lyons, C. T. Reinhard, N. J. Planavsky, The rise of oxygen in Earth's early ocean and atmosphere. *Nature* **506**, 307–315 (2014).
37. D. J. Burdige, *Geochemistry of Marine Sediments* (Princeton University Press, 2021).
38. F. Beulig, H. Røy, C. Glombitza, B. B. Jørgensen, Control on rate and pathway of anaerobic organic carbon degradation in the seabed. *Proc. Natl. Acad. Sci. U.S.A.* **115**, 367–372 (2018).
39. E. C. Laurenceau-Cornec *et al*., New guidelines for the application of Stokes' models to the sinking velocity of marine aggregates. *Limnol. Oceanogr.* **65**, 1264–1285 (2020).
40. F. A. C. Le Moigne *et al*., On the proportion of ballast versus non-ballast associated carbon export in the surface ocean. *Geophys. Res. Lett.* **39**, 1–6 (2012).
41. C. Lønborg, X. A. Álvarez–Salgado, R. T. Letscher, D. A. Hansell, Large stimulation of recalcitrant dissolved organic carbon degradation by increasing ocean temperatures. *Front. Mar. Sci.* **4**, 436 (2018).
42. C. Arnosti, B. B. Jørgensen, J. Sagemann, B. Thamdrup, Temperature dependence of microbial degradation of organic matter in marine sediments: Polysaccharide hydrolysis, oxygen consumption, and sulfate reduction. *Mar. Ecol. Prog. Ser.* **165**, 59–70 (1998).
43. A. Ridgwell, S. Arndt, *Why Dissolved Organics Matter: DOC in Ancient Oceans and Past Climate Change* (Elsevier Inc., ed. 2, 2015).
44. Y. Miyazaki, N. J. Planavsky, E. W. Bolton, C. T. Reinhard, Making sense of massive carbon isotope excursions with an inverse carbon cycle model. *J. Geophys. Res. Biogeosci.* **123**, 2485–2496 (2018).
45. L. A. Derry, A burial diagenesis origin for the Ediacaran Shuram-Wonoka carbon isotope anomaly. *Earth Planet. Sci. Lett.* **294**, 152–162 (2010).
46. S. Furuyama, A. Kano, Y. Kunimitsu, T. Ishikawa, W. Wang, Diagenetic overprint to a negative carbon isotope anomaly associated with the Gaskiers glaciation of the Ediacaran Doushantuo Formation in South China. *Precambrian Res.* **276**, 110–122 (2016).
47. D. H. Erwin *et al*., The Cambrian conundrum: Early divergence and later ecological success in the early history of animals. *Science* **334**, 1091–1097 (2011).
48. J. A. Cunningham, A. G. Liu, S. Bengtson, P. C. J. Donoghue, The origin of animals: Can molecular clocks and the fossil record be reconciled? *BioEssays* **39**, 1–12 (2017).
49. M. L. Droser, L. G. Tarhan, J. G. Gehling, The rise of animals in a changing environment: Global ecological innovation in the late Ediacaran. *Annu. Rev. Earth Planet. Sci.* **45**, 593–617 (2017).
50. D. H. Erwin, Early origin of the bilaterian developmental toolkit. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**, 2253–2261 (2009).
51. E. A. Sperling, J. Vinther, A placozoan affinity for *Dickinsonia* and the evolution of late Proterozoic metazoan feeding modes. *Evol. Dev.* **12**, 201–209 (2010).
52. G. J. Retallack, Were the Ediacaran fossils lichens? *Paleobiology* **20**, 523–544 (1994).
53. M. L. Droser, J. G. Gehling, The advent of animals: The view from the Ediacaran. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 4865–4870 (2015).
54. R. Wood *et al*., Integrated records of environmental change and evolution challenge the Cambrian Explosion. *Nat. Ecol. Evol.* **3**, 528–538 (2019).
55. G. M. Narbonne, Modular construction of early Ediacaran complex life forms. *Science* **305**, 1141–1144 (2004).
56. T. H. Boag, S. A. F. Darroch, M. Laflamme, Ediacaran distributions in space and time: Testing assemblage concepts of earliest macroscopic body fossils. *Paleobiology* **42**, 574–594 (2016).
57. T. H. Boag, R. G. Stockey, L. E. Elder, P. M. Hull, E. A. Sperling, Oxygen, temperature and the deep-marine stenothermal cradle of Ediacaran evolution. *Proc. Biol. Sci.* **285**, 20181724 (2018).
58. M. Laflamme, G. M. Narbonne, Ediacaran fronds. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **258**, 162–179 (2008).
59. A. V. Quinlan, The thermal sensitivity of generic Michaelis-Menten processes without catalyst denaturation or inhibition. *J. Therm. Biol.* **6**, 103–114 (1981).
60. A. V. Quinlan, The thermal sensitivity of Michaelis-Menten kinetics as a function of substrate concentration. *J. Franklin Inst.* **310**, 325–342 (1980).
61. C. M. Marsay *et al*., Attenuation of sinking particulate organic carbon flux through the mesopelagic ocean. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 1089–1094 (2015).
62. H. W. Ducklow, D. A. Hansell, J. A. Morgan, Dissolved organic carbon and nitrogen in the western Black Sea. *Mar. Chem.* **105**, 140–150 (2007).
63. S. Becquevort *et al*., The seasonal modulation of organic matter utilization by bacteria in the Danube-Black Sea mixing zone. *Estuar. Coast. Shelf Sci.* **54**, 337–354 (2002).
64. P. Albéric, E. Viollier, D. Jézéquel, C. Grosbois, G. Michard, Interactions between trace elements and dissolved organic matter in the stagnant anoxic deep layer of a meromictic lake. *Limnol. Oceanogr.* **45**, 1088–1096 (2000).
65. E. Bura-Nakić, E. Viollier, D. Jézéquel, A. Thiam, I. Ciglenečki, Reduced sulfur and iron species in anoxic water column of meromictic crater Lake Pavin (Massif Central, France). *Chem. Geol.* **266**, 311–317 (2009).
66. M. Karaca, A. Wirth, M. Ghil, A box model for the paleoceanography of the Black Sea. *Geophys. Res. Lett.* **26**, 497–500 (1999).