INTRODUCTION

The first-order features of Earth’s biosphere have undergone fundamental transformations over time. In particular, the structure and composition of surface ocean ecosystems and the metabolic and taxonomic affinities of dominant primary producers have changed dramatically. Initial primary producing communities on Earth would have been composed entirely of anoxygenic photosynthetic bacteria (Olson, 2006; Xiong, Fischer, Inoue, Nakahara, & Bauer, 2000), and for much of Earth’s subsequent history, cyanobacteria are thought to have been the principal oxygenic photosynthesizer (Falkowski et al., 2004; Johnston, Wolfe-Simon, Pearson, & Knoll, 2009; Knoll, 2014). Eukaryotes are generally thought to have evolved relatively early—almost 2,000 million years ago (Ma) (Knoll, 2014). The oldest likely eukaryotic microfossils occur in the latest Paleoproterozoic Changzhougou (~1,800 Ma) and Chuanlinggou (~1,700 Ma) Formations of North China (Lamb, Awramik, Chapman, & Zhu, 2009; Peng, Bao, & Yuan, 2009). The oldest definitive eukaryotic microfossils—forms such as Shuiyousphaeridium, Tappania, Satka, and Valeria, characterized by morphological complexity, large size, and encystment structures—occur in the latest Paleoproterozoic–early Mesoproterozoic (~1,800–1,600 Ma) Ruyang Group of China (Pang, Tang, Yuan, Wan, & Xiao, 2015) and the Mesoproterozoic
However, eukaryotic organisms do not become a key component of surface ocean ecosystems until much later in Earth's history (Figure 1), with no evidence of an important role for eukaryotic algae in primary production or of significant trophic structure in eukaryotic ecosystems emerging until after ~800 Ma (Brocks et al., 2017; Cohen & Macdonald, 2015; Gueneli et al., 2018; Laakso & Schrag, 2014, 2017; Zumberge et al., In press). Although it is possible that some of the earliest eukaryotic fossils are from stem groups that did not produce sterols (Porter, Agic, & Riedman, 2018), the nearly billion-year gap between the Mesoproterozoic emergence of bona fide eukaryotic microfossils and the appearance of eukaryote-produced steranes in the Neoproterozoic is typically linked to environmental inhibition of eukaryotes through most of Proterozoic time (Brocks et al., 2017).

As a backdrop to this ecological and evolutionary history, marine surface environments have also evolved considerably over time. The abundance of oxygen (O2) in Earth's ocean–atmosphere system has steadily and significantly increased through Earth's history (Holland, 1984; Kump, 2008; Lyons, Reinhard, & Planavsky, 2014). In addition, there is complementary evidence from the rock record and biogeochemical models that the inventory of dissolved phosphorus (P) in Earth's oceans has increased throughout Earth's history (Figure 1), broadly in step with the protracted oxygenation of the ocean–atmosphere system (Laakso & Schrag, 2014, 2017; Lenten & Watson, 2004; Ozaki, Reinhard, & Tajika, 2019; Papineau, 2010; Planavsky et al., 2010; Reinhard et al., 2017). Existing empirical records suggest that global rates of primary productivity (and by inference marine nutrient levels) during some periods of the mid-Proterozoic (~1.8–0.8 billion years ago, Ga) were likely less than ~10% of the modern Earth (Crockford et al., 2018), which is also consistent with global biogeochemical models of the coupled carbon and oxygen cycles for this time interval (Derry, 2015; Laakso & Schrag, 2018; Ozaki et al., 2019).

In theory, a link should exist between increases in marine P inventories and significant shifts in ecosystem structure. Both low-order idealized treatments (e.g., Armstrong, 1994, 1999) and large-scale mechanistic models (e.g., Ward, Dutkiewicz, & Follows, 2014; Ward, Dutkiewicz, Jahn, & Follows, 2012) predict that the availability of nutrients plays an important “bottom-up” role in controlling marine ecosystem structure and trophic complexity. Specifically, the basic features of modern plankton biogeography and size spectra can be reproduced reasonably well in theoretical models by assuming only that small phytoplankton cells have high nutrient affinities and are capable of rapid growth and that population-level rates of mortality in phytoplankton are density-dependent. Several important predictions for surface ocean ecosystems emerge from these principles. When considering only growth and nutrient utilization, smaller (e.g., cyanobacterial) cells should outcompete larger (e.g., photosynthetic eukaryotic, or algal) cells essentially everywhere, because their smaller sizes correspond to higher growth rates and greater affinity for limiting nutrients (though exceptions to this might occur in highly perturbed/seasonal environments). Algal abundance in modern oceans is therefore generally linked to a “top-down” (grazing) control on the abundance of smaller cells—which acts to prevent smaller primary producers from sequestering all of a limiting resource—while total biomass within the system is controlled by nutrient supply (Knoll & Follows, 2016; Price, Ahner, & Morel, 1994; Ward et al., 2014). As a result, increasing nutrient supply can balance grazing pressure at progressively larger phytoplankton size classes, resulting in a broader size spectrum, greater scope for the population of higher trophic levels, and greater overall biomass in the ecosystem. Conversely, severely nutrient-limited systems should come to be dominated by small phytoplankton cells, with little overall biomass and limited scope for the development of predation and higher trophic structure.

Here, we use a size-structured marine ecosystem model, embedded in an Earth system model of intermediate complexity (cGENIE) and configured for an illustrative interval of late Proterozoic time, to explore the impact of marine nutrient abundance on trophic structure and algal cell size. We find that the chronic P limitation characteristic of most of Earth's history (Bjerrum & Canfield, 2002; Derry, 2015; Jones, Nomosatryo, Crowe, Bjerrum, & Canfield, 2015; Laakso & Schrag, 2014, 2017, 2018; Ozaki et al., 2019; Planavsky, 2015; Reinhard et al., 2017) would have yielded generally small phytoplankton cell size, limiting the trophic scope of early eukaryotic ecosystems in surface ocean environments and attenuating production and export of biomass from the photic zone. Building on this framework, we suggest that the temporal correspondence between a significant shift in the Earth surface P cycle (Planavsky et al., 2010; Reinhard et al., 2017), the expansion of eukaryotic algae (Brocks et al., 2017; Cohen & Macdonald, 2015; Gueneli et al., 2018; Isson et al., 2018), and increasing evidence of predation in surface ocean ecosystems (Porter, 2016; Porter, Meisterfeld, & Knoll, 2003) after nearly 1 billion years of apparent ecological stasis (Knoll, 2014) may have been a natural outcome of an increase in marine nutrient supply linked to the long-term oxygenation of Earth's ocean–atmosphere system.

## 2 | Model Description

### 2.1 | The cGENIE Earth system model

We employ a carbon-centric version of the Grid ENabled Integrated Earth system model (cGENIE), an Earth system model of intermediate complexity (EMIC) previously used to explore links between climate and ocean biogeochemistry on a range of timescales (Cui et al., 2011; Gibbs et al., 2016; Gutjahr et al., 2017; Kirtland Turner & Ridgwell, 2016; Meyer, Kump, & Ridgwell, 2008; Monteiro, Pancost, Ridgwell, & Donnadieu, 2012; Olson, Reinhard, & Lyons, 2016; Panchuk, Ridgwell, & Kump, 2008; Reinhard, Planavsky, Olson, Lyons, & Erwin, 2016; Ridgwell, 2007; Ridgwell & Schmidt, 2010).
The ocean physics and climate model in cGENIE are comprised of a reduced physics (frictional geostrophic) 3-D ocean circulation model, coupled to a 2-D energy–moisture balance model (EMBM) and a dynamic–thermodynamic sea ice model. The ocean transports heat, salinity, and a suite of biogeochemical tracers, exchanges heat and moisture with the atmosphere, sea ice, and land and is forced at the ocean surface by the input of zonal and meridional wind stress by an imposed wind field. The EMBM considers heat and moisture balance within the atmospheric boundary layer, with air temperature and specific humidity as prognostic tracers. Moisture and heat are mixed horizontally throughout the 2-D atmosphere and are exchanged with the ocean and land surface with precipitation occurring above a prescribed threshold in relative humidity. The sea ice model tracks the horizontal transport of sea ice and the exchange of heat and freshwater with the ocean and atmosphere using ice thickness, areal fraction, and concentration as prognostic variables. Full descriptions of the model and coupling procedure can be found in Edwards and Marsh (2005) and Marsh, Müller, Yool, and Edwards (2011).

The biogeochemical model regulates air–sea gas exchange and the partitioning and transformation of biogeochemical tracers and isotopes within the ocean and atmosphere. By default, the ocean biological pump is driven by an "implicit" scheme in which a parameterized uptake of nutrients occurs in the surface ocean, followed by stoichiometric conversion to dissolved or particulate organic matter for downstream transport, sinking, and remineralization (Ridgwell et al., 2007). Dissolved organic matter is transported by the ocean model and decays with a prescribed time constant, while particulate organic matter is immediately exported out of the surface ocean and is partitioned into two fractions of differing lability. In the ocean interior, particulate
organic matter is remineralized instantaneously throughout the water column following an exponential decay function with a specified remineralization length scale for each fraction. The biological pump and inorganic carbon cycle within cGENIE, as well as the approach toward parameter calibration through data assimilation of modern tracer climatology, are described in detail in Ridgwell et al. (2007).

2.2 | EcoGEnIE: A size-structured ecological model

We replace the default implicit scheme of stoichiometric conversion of nutrients to organic matter in the surface ocean within cGENIE with a recently developed ecological model that explicitly resolves a size-structured plankton community—EcoGEnIE (Ward et al., 2018). The EcoGEnIE model distinguishes a prescribed number of plankton populations (Figure 2) that are defined based on their trophic functionality (e.g., Phytoplankton, Zooplankton, Mixotroph) and organism size (equivalent spherical diameter, ESD). These features then regulate the ecophysiological traits of each plankton group, such as rates of growth (e.g., nutrient uptake), grazing, and mortality. Phytoplankton growth and nutrient uptake are co-limited by nutrient availability, light, and temperature, where both the maximum rate of nutrient uptake and overall nutrient affinity are dependent on the Phytoplankton size (Armstrong, 1994, 1999; Moloney & Field, 1989, 1991; Ward et al., 2014, 2012) and functional group.

Zooplankton predation (grazing) scales with temperature and the abundance of potential prey biomass and is constrained by a maximum grazing rate that is size-dependent (here, we use “Zooplankton” to mean all plankton engaging in heterotrophy). The availability of potential prey is described as a roughly log-normal function of the predator-to-prey length ratio, with Zooplankton predominantly grazing on prey that are ~ 10 times smaller (Figure 2). Predators may also engage in “active switching” (Kiørboe, 2011; Kiørboe, Siaz, & Viitasalo, 1996; Vallina, Ward, Dutkiewicz, & Follows, 2014), preferentially grazing on prey that are relatively more available. Prey is assimilated into predator biomass with an efficiency for each element that is based on the respective predator quota for that element, leading to some fraction of prey biomass that is lost to the organic matter pool as a result of “messy feeding” (Hygum, Petersen, & Søndergaard, 1997; Møller, 2005). All living biomass is subjected to a linear mortality rate, with plankton mortality reduced at biomass levels below ~ 10⁻⁶ mmolC m⁻³ such that a viable population is maintained within every surface grid cell of the ocean model (Ward et al., 2018). This biomass level is sufficiently small it does not significantly impact other components of the ecosystem or the abundance and transformation of biogeochemical tracers.

The basic approach is to initialize the model with dissolved phosphate (PO₄³⁻) inventories ranging from 1% to 200% of the present oceanic level (POL; e.g., 1 POL represents a mean PO₄³⁻ inventory of 2.16 µmol/kg) and spin the model up to steady state for

![Figure 2](image-url)
10,000 years, allowing 3-D nutrient distributions within the ocean to come into equilibrium with the background climate state and marine plankton ecology. Our default ecosystem configuration—referred to here as the “2-guild” model (Table 1)—includes a total of 16 plankton size classes, with 8 size classes each of Phytoplankton and Zooplankton covering a size range between 200 nm and 1.9 mm (equivalent spherical diameter; ESD), similar to that explored in Ward et al. (2018). In this configuration, Phytoplankton and Zooplankton are strictly autotrophic or heterotrophic, respectively. We also evaluate an ensemble using a “Mixotroph” configuration in which the same size range as our default ensemble is spread across 9 Mixotrophic size classes, which can use light and inorganic nutrients autotrophically and also ingest prey (Table 2). This strategy is common in the modern ocean (Hartmann et al., 2012; Jones, 2000; Sanders, 1991; Stoecker, Hansen, Caron, & Mitra, 2017; Ward & Follows, 2016) and has been shown to have potentially significant impacts on carbon, nutrient, and energy fluxes through marine and freshwater ecosystems (Tittel et al., 2003; Ward & Follows, 2016). Lastly, we evaluate an ensemble with 64 total plankton size classes (“n64”), distributed evenly between 32 Phytoplankton and 32 Zooplankton (Table 3), in order to examine the impact of a less “quantized” size distribution.

2.3 Late cryogenian configuration of cGENIE

Because our main goal was to explore the factors leading to the rise in abundance of larger eukaryotic organisms in marine ecosystems, we employ a roughly late Cryogenian configuration of cGENIE. The ocean bathymetry and land–sea mask are derived from the 635 Ma configuration of Goddéris et al. (2017). Solar luminosity is calculated according to Gough (1981) (see also Feulner, 2012) and is set to 1,295.97 W/m² (i.e., a reduction of 5.3% relative to the modern value of 1,368 W/m²). In our “default” ensemble, atmospheric pCO₂ remains fixed at 3,336 ppm (~12 times the present atmospheric level, PAL), with surface wind fields that are derived offline from GCM simulations (Figure 3a). Similarly, we take a zonal mean planetary albedo profile directly from the coupled GCM simulations run at 3,336 ppm and apply it to cGENIE. We also explored the possible impact of background climate state by running two additional variable nutrient ensembles with the default (2-guild) plankton configuration. First, we perform a series of simulations with an elevated atmospheric pCO₂ of 20 PAL, sufficient to significantly increase sea surface temperatures both locally (Figure 3g–i) and in the global average (with mean sea surface temperature (SST) increasing from 18.9°C to 20.8°C). We then perform the same set of simulations at a reduced atmospheric pCO₂ of 3 PAL, sufficient to significantly decrease mean SST from 18.9°C to 14.3°C, expand austral sea ice coverage, and nucleate boreal sea ice, but without initiating a “snowball Earth” glaciation (Figure 3d–f).

The ocean model in all simulations is configured as a 36 × 36 equal-area grid (uniform in longitude and uniform in the sine of latitude) with 16 logarithmically spaced depth levels and seasonal surface forcing from the EMBM. Mean ocean salinity in the model is initialized at 33.9 PSU (~1 PSU lower than modern), consistent with an ice-free climate state at ~635 Ma. All simulations assume a fixed atmospheric pCO₂ of 10% PAL, and an initial ocean dissolved sulfate (SO₄²⁻) inventory of 1 mmol/kg. In the absence of good alternative constraints, the mean Mg/Ca ratio of the ocean is maintained at the modern value (10.28 mmol/kg Ca²⁺ and 52.82 mmol/kg Mg²⁺). Ocean biogeochemistry is initialized with a homogeneous distribution of tracers and plankton biomass, and the model is spun up for 10,000 years to ensure attainment of steady state. All model results shown here are annual averages from the last model year. The model code plus all configuration

### Table 1: Plankton size distribution and functional designations for plankton classes for the default (“2-guild”) ecosystem configuration. Sizes refer to the equivalent spherical diameter (ESD) of plankton cells.

<table>
<thead>
<tr>
<th>j</th>
<th>Functional type</th>
<th>ESD (µm)</th>
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<tbody>
<tr>
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<tr>
<td>2</td>
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</tr>
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<td>7</td>
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</tr>
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<td>8</td>
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</table>

### Table 2: Plankton size distribution and functional designations for plankton classes for the Mixotroph-only (“mixo”) ecosystem configuration. Sizes refer to the equivalent spherical diameter (ESD) of plankton cells.

<table>
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</tbody>
</table>
files and parameter values needed to run the simulations reported here are provided together with full instructions on GitHub (see Code Availability).

3 | RESULTS

We find that changes in the marine phosphate inventory have a significant impact on the distribution of different plankton size classes in the surface ocean in our 2-guild model of the Proterozoic Earth (Figure 4). At an ocean nutrient inventory characteristic of the modern Earth (Figure 4g-i), smaller Phytoplankton size classes (picoPhytoplankton, < 2 µm in diameter, and nanoPhytoplankton, 2–20 µm in diameter) are present at significant biomass throughout the global surface ocean, while the largest Phytoplankton size classes (microPhytoplankton, > 20 µm in diameter) remain restricted to higher latitudes. This distribution is essentially that of the contemporary surface ocean. In contrast, at a global ocean nutrient inventory equivalent to 10% POL (Figure 4d-f) picoPhytoplankton tend to be evenly distributed globally, with populations of nanoPhytoplankton abundant only at high latitudes and with microPhytoplankton biomass essentially negligible on a global scale. Further decreasing the ocean nutrient inventory to 1% POL results in negligible biomass within both nanoPhytoplankton and microPhytoplankton size classes and restricts picoPhytoplankton to high latitudes where vertical exchange with deep ocean nutrients is enhanced (Figure 4a-c). These changes in distribution are accompanied by significant decreases in mean and maximum Phytoplankton cell size and a dramatic drop in the overall size of Earth’s autotrophic biosphere (Figure 5).

<table>
<thead>
<tr>
<th></th>
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<th>ESD (µm)</th>
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**TABLE 3** Plankton size distribution and functional designations for plankton classes in the 32 × 32 (“n64”) ecosystem configuration. Sizes refer to the equivalent spherical diameter (ESD) of plankton cells.
The results of our ensemble of Earth system/marine ecosystem model simulations suggest that as ocean nutrient inventories increase, the expansion of biomass into progressively larger size classes (and, implicitly, an expansion of the importance of eukaryotic Phytoplankton relative to photosynthetic bacteria) has dramatic effects on the trophic scope of surface ocean ecosystems. To illustrate this, we analyze the abundance and distribution of the 190 µm Zooplankton size class (and the same Mixotrophic size class in our “Mixotroph-only” model), using this as a trophic proxy for early eukaryotic predators such as relatively small planktonic rhizarians and other ecologically similar eukaryotic micropredators (Andersen et al., 2016; Porter, 2016). We do not mean to suggest that a given size class corresponds precisely to any particular clade or that substantial eukaryotic trophic complexity cannot exist within smaller size classes (i.e., picoeukaryotes; Massana, 2011). Nevertheless, we consider this portion of the size spectrum to be a reasonable ecological “proxy” for the appearance of relatively large eukaryotic predators in the fossil record (Porter, 2016; Porter & Knoll, 2000).

We find that the distribution of the 190 µm size class is severely restricted below nutrient levels of ~10% those of the modern Earth for both our 2-guild and Mixotroph-only models (Figure 6a-d). We also find that for any given ocean nutrient inventory, Mixotrophy enhances the transfer of nutrients and biomass through planktonic ecosystems, supporting relatively greater biomass in larger size classes at a given set of conditions relative to the 2-guild model (Figure 6). This is consistent with previous work exploring the potential role of Mixotrophy in amplifying carbon and energy fluxes through modern marine ecosystems (Ward & Follows, 2016). However, the overall magnitude of this difference decreases sharply at progressively lower ocean nutrient inventories, and even entirely, Mixotrophic biospheres show limited capacity to support large eukaryotic predator biomass at estimated Proterozoic nutrient inventories (Figures 6, 7).
In order to estimate the impact of marine nutrient inventory on the abundance of large predatory eukaryotes on a global scale, we calculate the total integrated plankton biomass present in the 190 µm size class for the default (“2-guild”), Mixotroph-only (“mixo”), and 64 size class (“n64”) configurations and compare this with available estimates for ocean nutrient levels during Proterozoic time (Figure 7). Overall biomass (and thus implicitly the scope for large eukaryotic predators) are severely curtailed in our models at estimated Proterozoic ocean nutrient levels based on the geochemistry of iron-rich marine sedimentary rocks (Jones et al., 2015) and large-scale biogeochemical models (Laakso & Schrag, 2017; Ozaki et al., 2019; Reinhard et al., 2017). Trophic transfer to predatory size classes is enhanced in the Mixotroph-only model, but our model predicts that the effect of this on a global scale would have been very small at estimated ocean nutrient levels during the Proterozoic. There is a coherent, though relatively small, increase in Zooplankton predator atmospheric pCO2 drops, which we attribute to decreased nutrient utilization at colder temperatures with more extensive sea ice coverage near the poles. However, the effect is small, with all ensembles showing the same sharp increase in globally integrated Zooplankton predator biomass at oceanic nutrient inventories significantly above ~10% that of the modern Earth (Figure 7).

4 | DISCUSSION

Our model results suggest that changes in the ocean nutrient inventory during Proterozoic time may have exerted significant leverage...
over marine trophic structure and the evolutionary ecology of early eukaryotes. However, a number of interesting issues remain to be explored in similar models and grounded in observations from the geologic record. For example, we do not explicitly link the strength of the biological pump to Phytoplankton cell size, and we anticipate that expansion of the plankton size structure will feed back into ocean redox structure and surface nutrient availability on timescales of \( \sim 10^2 \)–\( 10^4 \) years. These changes would be further modulated by shifts in the biomass C/P ratio of primary producers driven by changes to nutrient availability and trophic structure (Deutsch & Weber, 2012; Moreno & Martiny, 2018; Reinhard et al., 2017), all of which will feed back into the global carbon and oxygen cycles on timescales that scale to some extent with atmospheric \( pO_2 \) but approach \( \sim 10^6 \) years when atmospheric \( pO_2 \) is relatively high (Holland, 1984). Finally, while our model results provide persuasive evidence for the centrality of marine P levels in controlling ecosystem structure, they are incapable of constraining the mechanistic drivers that may have led to significant shifts in P cycling during the late Proterozoic.

Nevertheless, our model results provide a simple explanation for the macroevolutionary lag between the initial appearance of total- and crown-group eukaryotes in the microfossil record (Javaux, Knoll, & Walter, 2001; Javaux et al., 2004; Knoll, Javaux, Hewitt, & Cohen, 2006; Lamb et al., 2009), and as predicted from molecular clocks (Betts et al., 2018; Parfrey, Lahr, Knoll, & Katz, 2011), and the much later expansion of eukaryotic algae, micro-predators, and more complex heterotrophs observed in the molecular biomarker, microfossil, genomic, and geochemical records (Cohen & Macdonald, 2015; Gold et al., 2016; Gueneli et al., 2018; Isson et al., 2018; Knoll, 2014; Love et al., 2009; Porter et al., 2003; Zumberge et al., In press). In addition, these results provide persuasive additional evidence for a straightforward mechanistic link between changes to ocean nutrient levels and the "rise of algae" during late Proterozoic time (Brocks et al., 2017; Zumberge et al., In press), in which increasing availability of P to surface marine ecosystems allowed for an expansion in the size spectra of autotrophs and increased trophic scope among larger eukaryotic predators (including sponge-grade metazoans; Love et al., 2009; Zumberge et al., 2018). This style of trophic escalation, driven by increasing nutrient availability, has been previously invoked to explain changes to molecular biomarker assemblages and stable isotope compositions (Brocks et al., 2017; Gueneli et al., 2018) and turnover of eukaryotic acritarch lineages during the late
Proterozoic (Knoll, 1994; Vidal & Moczydlowska-Vidal, 1997). Our results support this and provide a series of spatially explicit predictions that can be further tested against more detailed paleontological and geochemical records.

Our results also provide a new perspective on the potential mechanistic links between ocean–atmosphere oxygenation on Earth and the ecological expansion of animal life, as they suggest that a relatively large ocean nutrient inventory is a prerequisite for the upstream ecological expansion of larger, more complex organisms in benthic habitats. Indeed, limited carbon delivery to the benthic realm may have been a central ingredient in the confluence of ecological factors constraining early metazoan communities (Sperling & Stockey, 2018). Low nutrient levels are in turn thought to be strongly impacted by surface oxygen levels and the marine redox landscape (Derry, 2015; Jones et al., 2015; Laakso & Schrag, 2014; Reinhard et al., 2017), providing a direct but previously unrecognized mechanistic link between ocean–atmosphere O₂ abundance and the evolutionary ecology of early animal life. In particular, the levels of ocean–atmosphere O₂ required to support large ocean nutrient inventories may be significantly different from those required for the resting and/or active metabolisms of basal aerobic metazoans. Indeed, the estimated O₂ requirements of early animals are potentially very low (Mills et al., 2014; Sperling, Halverson, Knoll, Macdonald, & Johnston, 2013), while the atmospheric O₂ levels required to maintain large ocean nutrient inventories may be considerably higher (Laakso & Schrag, 2014; Reinhard et al., 2017). Fully constraining the offset between these two surface O₂ levels and their potential impacts on ocean chemistry and evolution remains an important task for future work. In any case, our results suggest that the sharp rise in eukaryotic diversification and the complexity of surface ocean ecosystems during the late Proterozoic may have been mechanistically linked to changes in ocean redox structure, nutrient availability, and atmospheric O₂ abundance.

5 | CONCLUSIONS

If existing estimates of Proterozoic marine nutrient levels are correct, our model results indicate that shifts in Earth’s phosphorus cycle during late Proterozoic time would have resulted in dramatic changes in the scope for upward energy flow and eukaryotic predation in ocean ecosystems. These shifts would be predicted to have significant downstream impacts on carbon and energy fluxes to the benthic realm, linking marine nutrient abundance to the ecology of early animal life. Our results also imply a novel, though indirect, link between the abundance of O₂ in Earth’s atmosphere and the trophic scope of marine ecosystems, through the relationships that link ocean–atmosphere O₂ and Earth’s phosphorus cycle on geologic timescales. When considered in light of progressively more quantitatively precise and stratigraphically continuous empirical constraints on marine nutrient abundance and ocean–atmosphere oxygenation, spatially explicit modeling of planktonic ecosystems has the potential to provide important insight into the environmental context for the emergence and expansion of biological complexity on the late Proterozoic Earth.

6 | CODE AVAILABILITY

A manual describing code installation, basic model configuration, and an extensive series of tutorials is provided. The LaTeX source of the manual and PDF file can be obtained by cloning (https://github.com/derpycode/muffindoc). The user manual contains instructions for obtaining, installing, and testing the code, as well as running experiments. The version of the code used in this paper is tagged as release v0.9.9 and has a DOI of 10.5281/zenodo.3620841. Configuration files for the specific experiments presented in the paper can be found in: cgenie.muffin/genie-user-configs/MS/reinhardetal.Geobiology.2020. Details of the different experiments, plus the command line needed to run each, are given in README.txt.

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CONFLICT OF INTERESTS
The authors declare no competing interests.

AUTHOR CONTRIBUTIONS
C.T.R. and N.J.P. designed the study. G.L.H. and A.R. developed the default Cryogenian climate configuration for cGENIE. C.T.R. carried out the cGENIE simulations and all data analysis. C.T.R. led the writing of the paper with additional input from all authors.

DATA AVAILABILITY STATEMENT
All model code and configuration files will be made available during publication via GitHub.

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