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# 1 Possible patterns of marine primary productivity during the Great Ordovician 2 Biodiversification Event

3  
4 Alexandre Pohl, David A.T. Harper, Yannick Donnadiou, Guillaume Le Hir, Elise  
5 Nardin & Thomas Servais

## 6 Abstract

7 Following the appearance of numerous animal phyla during the ‘Cambrian Explosion’, the ‘Great  
8 Ordovician Biodiversification Event’ (GOBE) records their rapid diversification at the lower taxonomic  
9 levels, constituting the most significant rise in biodiversity in Earth’s history. Recent studies suggest  
10 that the rapid rise in phytoplankton diversity observed at the Cambrian–Ordovician boundary may  
11 have profoundly restructured marine trophic chains, paving the way for the subsequent flourishing  
12 of plankton-feeding groups during the Ordovician. Unfortunately, the fossil record of plankton is  
13 incomplete. Its smaller members represent the bulk of the modern marine biomass, but they are  
14 usually not documented in Palaeozoic sediments, preventing any definitive assumption with regard  
15 to an eventual correlation between biodiversity and biomass at that time. Here we use an up-to-date  
16 ocean general circulation model with biogeochemical capabilities (MITgcm) to simulate the spatial  
17 patterns of marine primary productivity throughout the Ordovician, and we compare the model  
18 output with available palaeontological and sedimentological data.– 160/250 words –

19  
20  
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29 France.

## 30 Introduction

31

32 The 'Great Ordovician Biodiversification Event' (GOBE) was arguably the most important and  
33 sustained increase of marine biodiversity in Earth's history (e.g. Sepkoski 1995; Webby 2004; Harper  
34 2006). During the so-called 'Cambrian explosion' most, if not all, animal phyla first appeared in the  
35 fossil record. Subsequently, during the Ordovician Period, an 'explosion' of diversity at the order,  
36 family, genus, and species level occurred.

37

38 The search for the triggers of this biodiversification is ongoing, but most probably there was no  
39 unique cause, but the combined effects of several geological and biological processes that helped  
40 generate the GOBE.

41

42 During the Ordovician Period, a unique palaeogeographical scenario existed, with the greatest  
43 continental dispersal of the Palaeozoic. High sea levels that were the highest during the Palaeozoic, if  
44 not of the entire Phanerozoic, allowed marine waters to cover large epicontinental areas and flooded  
45 large tropical shelf areas, enabling diversification (e.g. Servais *et al.* 2009, 2010). The climate was  
46 warm, although recent studies indicate a significant, long cooling trend throughout the Ordovician,  
47 followed up by an abrupt cooling at the end of the period, triggering the Late Ordovician glacial peak  
48 (Trotter *et al.* 2008, Nardin *et al.* 2011, and Harper *et al.* 2014).

49

50 During the Ordovician, important ecological evolutionary changes occurred, beginning with the  
51 'explosion' of the phyto- and zooplankton, leading to the 'Ordovician plankton revolution' (Servais *et al.*  
52 2008). The onset of the GOBE is actually, at least partly for the planktonic groups, rooted in the  
53 late Cambrian, when most of the planktonic organisms started to rapidly diversify (Servais *et al.*  
54 2016). In this context, Saltzman *et al.* (2011) already considered that during the latest Cambrian a  
55 major increase of atmospheric oxygen concentration ( $pO_2$ ) had already taken place. The temporal  
56 correlation between the Cambrian oxygenation event and the concomitant rise in plankton diversity  
57 led Saltzman *et al.* (2011) and Servais *et al.* (2016) to hypothesize that the increase of  $pO_2$  might have  
58 triggered the increase of plankton diversity, which may be related to changes in macro- and  
59 micronutrient abundances in increasingly oxic marine environments. The higher amount of available  
60 nutrients in the oceans possibly triggered the development of pico- and phytoplankton, i.e. the basis  
61 of modern marine trophic chains (Saltzman *et al.* 2011; Servais *et al.* 2016). Logically, the trophic  
62 chain is then assembled with additional tiers provided by the suspension-feeding benthos (e.g.,  
63 brachiopods, bryozoans and corals) and nekton, themselves prey to a range of predators, including  
64 the trilobites, with orthoconic cephalopods and fishes at and near the top of the food chain.

65

66 Great advances have been made during the last decades concerning palaeogeographical

67 reconstructions for the Early Palaeozoic, including the Ordovician (e.g. Torsvik & Cocks 2013). These  
68 more reliable global palaeogeographical reconstructions have allowed the formulation of simple  
69 conceptual and more complex numerical models for ancient atmospheric and ocean circulation  
70 patterns, or to hypothetically locate upwelling zones (e.g. Wilde, 1991; Christiansen & Stouge 1999;  
71 Hermann *et al.* 2004; Pohl *et al.* 2014 ; Servais *et al.* 2014). More recently, new constraints on the  
72 palaeobiogeography of marine living communities were provided by the publication of maps showing  
73 much more precisely the ocean surface circulation modelled at various atmospheric CO<sub>2</sub> levels during  
74 the Early, Middle and Late Ordovician (Pohl *et al.* 2016b).

75  
76 The aim of the present paper is to model possible patterns of biomass production in the Ordovician  
77 seas, in order to attempt to understand where and how the diversification originated. We use here  
78 an ocean-atmosphere general circulation model with biogeochemical capabilities (MITgcm) in order  
79 to simulate the changing spatial patterns of marine primary productivity in response to the  
80 palaeogeographical evolution throughout the Ordovician. We subsequently attempt to compare the  
81 model output with available palaeontological and sedimentological data.

82

## 83 **Ordovician biomass and the sedimentary record**

84

### 85 **Primary productivity in ancient oceans**

86 Many palaeontologists have focussed on the analyses of palaeobiodiversity during the Phanerozoic  
87 (e.g., Sepkoski *et al.* 1981; Alroy 2010; Harper *et al.* 2015). Such studies lead to the understanding of  
88 the major trends in biodiversification during Earth History, and to the discovery of the major  
89 extinction phases, including the Big-Five mass extinctions. Specialists in macroevolution and  
90 macroecology usually apply various statistical methods in order to better understand and interpret  
91 the changing palaeobiodiversities (e.g. Sepkoski 1995; Bambach 2006; Alroy 2010; Stanley 2016). The  
92 GOBE has also been recognized based on these studies.

93

94 Biodiversity is a measure of the number of biological organisms present at a given moment, but  
95 usually provides no information about the abundance of these organisms. Little attention has been  
96 paid to the evolution of the biomass in the oceans (e.g. Franck *et al.* 2006; Kallmeyer *et al.* 2012).  
97 Similarly, the evolution of the abundance of nutrients available in the oceans during the history of  
98 the Earth is only poorly known (e.g. Allmon & Martin 2014). In addition, biodiversity is not (at least  
99 not directly) linked to the biomass produced (Irigoiien *et al.* 2004; Finnegan & Droser 2008). As a  
100 result, little information is available about biomass, or the primary productivity in ancient oceans,

101 including that during the GOBE.

102

103 A few authors attempted to understand the evolution of the marine biomass during geological time.  
104 Martin (2003), for instance, analysed the fossil record of biodiversity in relation to nutrients,  
105 productivity and habitat area, whereas Martin *et al.* (2008) investigated the evolution of ocean  
106 stoichiometry (nutrient content) in order to understand the biodiversification of the Phanerozoic  
107 marine biosphere. Concerning the Ordovician, Payne & Finnegan (2006) considered that during the  
108 GOBE the increase in the complexity of the marine trophic chains and in the efficiency of marine  
109 organisms in removing available food, from both the water column and the sediment, appears to  
110 account for a secular increase in animal biomass. Based on Martin *et al.* (2008), Servais *et al.* (2016)  
111 further considered that the increasing presence of planktonic organisms in the late Cambrian – Early  
112 Ordovician must coincide with increasing nutrient supply, increased primary productivity and  
113 expanded biomass production, that resulted during the initiation of the GOBE with a higher diversity  
114 and increased abundance of plankton-feeding groups during the Ordovician. Nowak *et al.* (2015)  
115 effectively observed a dramatic increase in diversity of the acritarchs, i.e. the organic-walled fraction  
116 of the phytoplankton, in the late Cambrian – Early Ordovician interval. But do the higher diversities  
117 of phytoplanktonic organisms also indicate an increased abundance of phytoplankton, and an  
118 increased biomass?

119

120 Ocean productivity largely refers to the production of organic matter by ‘phytoplankton’ (e.g. Sigman  
121 & Hain 2012). In summary, most of the single-celled phytoplankton are ‘photoautotrophs’ that use  
122 nutrients and light to convert inorganic to organic carbon. They are subsequently consumed by the  
123 ‘heterotrophs,’ that include the ‘zooplankton,’ the ‘benthos,’ and the ‘nekton.’ The most important  
124 nutrients necessary for the phytoplankton are nitrogen (N), phosphorus (P), iron (Fe), and silicon (Si),  
125 while sunlight is the basic energy source needed. Until recently, it was assumed that the larger parts  
126 of the phytoplankton (between 5 and 100  $\mu\text{m}$  in diameter) account for most phytoplankton biomass  
127 and productivity. This larger phytoplankton is partly preserved in the fossil record, and corresponds  
128 in the Palaeozoic to the informal group of the acritarchs. However, recent studies indicate that more  
129 than half of the biomass in modern oceans is actually produced by the much smaller fraction ( $< 2 \mu\text{m}$   
130 in diameter), referred to the picoplankton (e.g. Buitenhuis *et al.* 2012). Recent estimates indicate  
131 that 30 % of the modern oceanic biomass is constituted by picoheterotrophs and 25 % of  
132 picophytoplankton (e.g., Buitenhuis *et al.* 2013; Moriarty & O’Brien 2013). This small fraction is  
133 almost entirely unknown from the fossil record, the picoplankton not being observed by  
134 palaeopalynologists because it falls out of the range of classical observational methods. However,  
135 most recent studies indicate that it is this fraction that is the most diverse in modern oceans (e.g., De

136 Vargas *et al.* 2015).

137

138 Thus, our understanding of the fossil record of the base of the trophic chain is highly incomplete in  
139 the Ordovician, as only a minor fraction of the phytoplankton is recorded under the informal  
140 grouping of, for example, the acritarchs. A key approach, therefore, to tentatively understand the  
141 biomass production in the Early Palaeozoic is numerical models. In the present study we apply such a  
142 model for three different time intervals in the Ordovician to tentatively understand marine  
143 productivity during the GOBE interval. Our analysis specifically focuses on large-scale upwelling  
144 systems, which generate high rates of biomass production and leave a distinctive fingerprint in the  
145 sedimentary record.

146

## 147 Secondary production in upwelling systems

148 Modern coastal upwelling zones have been a focus of investigation for a number of years as loci of  
149 bioproductivity. Here, benthic and nektonic diversity is influenced by a wide range of environmental  
150 factors together with low-oxygen concentrations and biotic interactions such as competition and  
151 predation. Upwelling zones promote bioproductivity through the delivery of nutrient-rich, deep  
152 water onto the shelf, igniting the growth and abundance of phytoplankton. During the GOBE and  
153 early stages of the establishment of the Palaeozoic Evolutionary Fauna, communities were  
154 dominated by suspension feeders such as the brachiopods, bryozoans and corals and potentially  
155 could benefit directly as primary consumers. There is a wealth of biodiversity data available for all  
156 the major benthic and nektonic groups (e.g. Webby *et al.* 2004) but there are relatively few regional  
157 studies related to specific geographic areas.

158

159 Recent studies of some of the key coastal upwelling zones, e.g. along the Namibian Coast (Eisenbrath  
160 & Zettler 2016), associated with the Benguela Current Large Marine Ecosystem (BCLME), together  
161 with those on coastal upwelling along the Peru coast (Rosenberg *et al.* 1983), the effects of El Niño  
162 on the benthos of the Benguela, California and Humboldt upwelling ecosystems (Arntz *et al.* 2006)  
163 and upwelling along the NW Africa coast (Thiel 1982) have established some key properties for these  
164 zones. Primary and secondary production is substantial, however, it also generates low-oxygen  
165 conditions commonly moving the Oxygen Minimum Zone (OMZ) into shallower-water environments.  
166 Biotas are dominated by soft-bodied taxa, there is a reduced diversity and evenness and fewer  
167 calcified forms (Levin 2003). In many cases assemblages are dominated by pioneer communities  
168 populated by opportunistic species forming dense accumulations. Moreover, the poor oxygen  
169 conditions encourage the migration of taxa into shallower water, extending too their geographic

170 ranges along the shelf. Organisms are abundant, generating substantial biomass but not necessarily  
171 high diversities.

172

## 173 **Methods: model description**

### 174 **Ocean, atmosphere and sea ice**

175 We used a coupled ocean-atmosphere-sea ice setup of the Massachusetts Institute of Technology  
176 general circulation model (MITgcm). An isomorphism between ocean and atmosphere dynamics is  
177 exploited to allow a single hydrodynamical core to simulate both fluids (Marshall *et al.* 2004). The  
178 oceanic and the atmospheric components also share the same cubed-sphere grid with 32 x 32 points  
179 per face (cs32), yielding a mean equatorial resolution of 2.8° x 2.8°. The cubed-sphere grid avoids  
180 polar singularities resulting from the convergence of the meridians at the poles, thus ensuring that  
181 the model dynamics there is treated with as much fidelity as elsewhere (Adcroft *et al.* 2004).

182 The oceanic component is an up-to-date, hydrostatic, implicit free-surface, partial step topography  
183 ocean general circulation model (Marshall *et al.* 1997*a, b*). Twenty-eight levels are defined vertically,  
184 the thickness of which gradually increases from 10 m at the surface to 1300 m at the bottom. Effects  
185 of mesoscale eddies are parameterised as an advective process (Gent & McWilliams 1990) and an  
186 isopycnal diffusion (Redi 1982). The nonlocal K-Profile Parameterisation (KPP) scheme of Large *et al.*  
187 (1994) accounts for vertical mixing in the ocean's surface boundary layer, and the interior. The  
188 atmospheric physics is based on the Simplified Parameterisations, Primitive-Equation Dynamics  
189 (SPEEDY) scheme (Molteni 2003). The latter comprises a four-band longwave radiation scheme, a  
190 parameterisation of moist convection, diagnostic clouds, and a boundary layer scheme. A low vertical  
191 resolution is used. Five levels are defined: one level represents the planetary boundary layer, three  
192 layers are placed in the troposphere and the fifth layer is placed in the stratosphere. The pressure  
193 coordinate  $p$  is employed. Sea ice is simulated using a thermodynamic sea-ice model based on the  
194 Winton (2000) two and a half layer enthalpy-conserving scheme. Sea-ice growth occurs when the  
195 ocean temperature falls below the salinity dependent freezing point.

196 Fluxes of momentum, freshwater, heat, and salt are exchanged every 20 minutes in the model (i.e.,  
197 the ocean time step). The resulting coupled model can be integrated for ca. 100 years in one day of  
198 dedicated computer time. Relatively similar model configurations were used in the past (Enderton &  
199 Marshall 2009; Ferreira *et al.* 2010; 2011), including those for palaeoceanographical purposes  
200 (Brunetti *et al.* 2015; Pohl *et al.* 2017).

### 201 **Primary productivity**



202 The MITgcm includes a biogeochemistry model that simulates the net primary productivity (NPP) in  
203 the ocean. NPP is computed based on Michaelis-Menten equations as a function of available  
204 photosynthetically active radiation (PAR) and phosphate concentration ( $PO_4$ ),

$$205 \quad NPP = \alpha \frac{PAR}{PAR + K_{PAR}} \frac{PO_4}{PO_4 + K_{PO_4}}$$

206 where  $\alpha = 2 \times 10^{-3} \text{ mol m}^{-3} \text{ yr}^{-1}$  is the maximum community productivity,  $K_{PAR} = 30 \text{ W m}^{-2}$  the half  
207 saturation light constant, and  $K_{PO_4} = 5 \times 10^{-4} \text{ mol m}^{-3}$  the half saturation phosphate constant. In this  
208 configuration, phosphate is the single limiting nutrient. It is consumed in the photic zone to fuel the  
209 marine primary productivity, regenerated by remineralisation throughout the water column based  
210 on the empirical law of Martin *et al.* (1987), redistributed within the ocean using the velocity and  
211 diffusivity fields provided by the general circulation model and ultimately returned back to the ocean  
212 surface in upwelling zones. Because phosphate is assumed to have an oceanic residence time much  
213 longer than the oceanic turnover time scale (i.e., 10–40 kyr; Ruttenberg 1993; Wallmann 2003), its  
214 global oceanic concentration is fixed in the model (Dutkiewicz *et al.* 2005). Iron is known as another  
215 major factor in productivity (Falkowski 2012). Because it is mainly delivered to the ocean surface as  
216 dust from deserts, the emissions of which are difficult to quantify today (Bryant 2013); providing the  
217 model with seasonal maps of iron input in the Ordovician is challenging. Although our  
218 biogeochemical model has the provision to account for cycling of iron, we prefer not to consider iron  
219 fertilisation here. The PAR is computed at the ocean surface as a fraction of the incident shortwave  
220 radiation provided by the atmospheric component of the MITgcm. It is then attenuated throughout  
221 the water column assuming a uniform extinction coefficient. Similar configurations of this  
222 biogeochemistry model have been used in the past (Friis *et al.* 2006; 2007), including those for the  
223 Ordovician (Pohl *et al.*, 2017).

## 224 **Boundary and initial conditions**

225 We ran our model on three palaeogeographical reconstructions representative of the Early  
226 Ordovician (480 Ma, Tremadocian), the Middle Ordovician (460 Ma, Darriwilian) and the early  
227 Silurian (440 Ma, Aeronian). The location of the continental masses is taken from the reconstructions  
228 by Torsvik & Cocks (2009). The topography and the bathymetry are reconstructed based on  
229 published global reconstructions, with additional information from regional studies for Gondwana  
230 (e.g. Torsvik & Cocks 2013), Laurentia (e.g. Cocks & Torsvik 2011), Baltica (e.g. Cocks & Torsvik 2005),  
231 Siberia (e.g. Cocks & Torsvik 2007) and Asia (e.g. Cocks & Torsvik 2013). Because the location and  
232 depth of Ordovician ocean ridges is not well constrained, they are not included in the model. We use  
233 a flat-bottom ocean, the depth of which is set to present-day mean seafloor depth, i.e., –4000 m

234 (Pohl *et al.* 2014). The flat bottom is not expected to constitute a major bias. Several studies on late  
235 Palaeozoic oceans suggest that it does not critically impact the large-scale patterns of simulated  
236 ocean circulation (Montenegro *et al.* 2011; Osen *et al.* 2012). The resulting palaeomaps are very  
237 similar to those used by Pohl *et al.* (Pohl *et al.* 2016b).

238 A gradual greening of the continents occurred throughout the Ordovician. The first, non-vascular  
239 land plants are documented from the Middle Ordovician Dapingian (Rubinstein *et al.* 2010). There is  
240 no evidence of plants on land before that date, including during the Tremadocian, i.e., the first time  
241 slice used in the present study. In addition, the spatial cover of this primitive vegetation is difficult to  
242 estimate for the remainder of the period (Edwards *et al.* 2015; Porada *et al.* 2016). As a consequence  
243 we here follow previous studies (Nardin *et al.* 2011; Pohl *et al.* 2014) and impose a rocky desert  
244 landscape on the continents (ground albedo of 0.24, which is potentially modified by snow).

245 During the Ordovician, the atmospheric partial pressure of CO<sub>2</sub> ( $p\text{CO}_2$ ) was significantly higher than  
246 today (e.g. Berner 2006). However, the MITgcm does not account for varying  $p\text{CO}_2$  levels. It is tuned  
247 to the present-day  $p\text{CO}_2$ . We therefore increased the solar forcing in the model to simulate various  
248 climatic states (Ferreira *et al.* 2011) and subsequently compared the simulated temperatures with  
249 Ordovician estimates. A solar constant of 350 W m<sup>-2</sup> (instead of 342 W m<sup>-2</sup> today) induces an increase  
250 in tropical sea-surface temperatures (SSTs) up to 32.5 °C to 33.7 °C (depending on the time slice  
251 considered). These values compare well with the SSTs reconstructed by Trotter *et al.* (2008) for the  
252 Middle Ordovician based on  $\delta^{18}\text{O}$  measurements (see their Fig. 3 in particular). Alternative values  
253 would better fit the Early and the Late Ordovician SSTs, but we here aim at quantifying the impact of  
254 the palaeogeographical changes on the spatial patterns of Ordovician primary productivity, all other  
255 things kept equal. We therefore conduct our three simulations using a solar constant of 350 W m<sup>-2</sup>,  
256 which are here selected to provide the best match with Middle Ordovician SST estimates. The orbital  
257 configuration is defined with an obliquity of 23.45° and an eccentricity of 0°.

258 We use identical initial conditions in all simulations, including an homogeneous salinity of 35 psu  
259 (practical salinity units) and a theoretical latitudinal gradient of ocean temperature characterised by  
260 equatorial and polar SSTs of respectively 35 °C and 6 °C and an ocean bottom potential temperature  
261 of 3 °C. These values ensure that the ocean is sea ice free at the beginning of each model run.  
262 Phosphate is initialised with its present-day depth profile. For each simulation, the physical ocean-  
263 atmosphere-sea ice model is first run until deep-ocean equilibrium is reached ( $\geq 2000$  model years).  
264 It is subsequently restarted with marine biogeochemistry for 550 additional years and climatic fields  
265 used for analysis are averaged over the last 50 years of the simulation.

266

## 267 **Results: simulated Ordovician marine productivity**

### 268 **In space: wind belts and Ekman pumping**

269 The main patterns of simulated Ordovician surface primary productivity (Fig. 1) reflect in simple  
270 terms the ocean phosphate concentration, while the PAR only imposes a hemispheric-scale decrease  
271 of NPP with latitude. The phosphate concentration in surface seawaters results, in turn, from the  
272 large-scale patterns of Ekman pumping. The concentration in  $\text{PO}_4$  is lower in shallow waters because  
273 nutrients are consumed during photosynthesis and it increases with depth due to remineralisation of  
274 sinking particles. Upwelling systems allow nutrient-rich deep waters to be transported back to the  
275 surface and they are therefore associated with locally high phosphate content. On the contrary,  
276 down welling areas are poor in nutrients. The spatial patterns of upwelling and down welling are  
277 essentially driven by the direction of the wind blowing over the ocean surface through Ekman  
278 pumping and suction. The Trade Winds induce large-scale upwelling systems on the western margin  
279 of tropical landmasses, and the Westerlies cause high phosphate concentrations at the mid-latitudes  
280 ( $40^\circ - 60^\circ$ ). Between the Trade Winds and the Westerlies, the down welling of surface waters along  
281 the tropics ( $30^\circ$ ) leads to low phosphate levels. A local minimum in phosphate concentration and  
282 thus primary productivity occurs in the Palaeo-Tethys, between the eastern coasts of Baltica and the  
283 western margin of tropical Gondwana (Fig. 1A-C). Here, the down welling of surface waters combines  
284 with a strong freshwater input from the continent. The latter results from the intense orographic  
285 precipitation that occurs when the moisture-laden Westerlies intercept the coastal topography of  
286 Gondwana. Pohl *et al.* (2017) demonstrated that this strong runoff to the ocean is a robust model  
287 result that it not overly model-dependent. While the polar latitudes ( $60^\circ - 90^\circ$ ) are dynamically  
288 isolated from the global ocean and thus depleted in phosphate in the Northern Hemisphere (Pohl *et*  
289 *al.* 2017), deep-water convection along the coast of Gondwana (e.g. Poussart *et al.* 1999; Herrmann  
290 *et al.* 2004) drives the local enrichment of surface waters in nutrients, ensuring relatively high  
291 productivity levels there.

292 Although the small-scale spatial patterns of simulated NPP may be model-dependent to some extent,  
293 the fact that the first-order signal results from a fundamental characteristic of Earth's climate (the  
294 zonal wind belts) suggests that these results are relatively robust (Pohl *et al.*, 2017).

### 295 **In time: throughout the Ordovician**

296 The three studied time slices share a certain number of common features (Fig. 1). The western  
297 margin of Laurentia, first, is associated with high levels of simulated NPP. In both hemispheres, the  
298 mid-latitudes are further characterised by zonal currents inducing Ekman pumping and the upwelling

299 of nutrients fuelling a strong productivity. On the contrary, low marine productivity levels typify the  
300 tropics (30°), the margin of Gondwana situated over the South Pole and the Northern high-latitudes.  
301 A local minimum persists throughout the period at 30° S between the western coast of Gondwana  
302 and the tropical landmasses.

303 Nevertheless, major changes can be observed from 480 Ma to 440 Ma (Fig. 1). The most considerable  
304 alteration of the NPP patterns between the Early and the Late Ordovician resulted from the gradual  
305 drift of Gondwana to the North. Confined in the Southern Hemisphere at 480 Ma, the supercontinent  
306 reached 30° N at 440 Ma. The direct consequence of this continental drift was the appearance of a  
307 major upwelling system at tropical latitudes in the Late Ordovician along the coasts of Gondwana  
308 (Australia and India) and South China-Annamia. The contrast between the eastern and western  
309 tropical coasts of Gondwana increased at the same time, with simulated NPP significantly decreasing  
310 along the eastern coast of Gondwana at 440 Ma. Elsewhere, the spatial patterns of simulated NPP  
311 remained relatively stable as the tropical continental masses slowly migrated to the North. This  
312 continental drift prompted Siberia to slowly shift, from the Early to the Late Ordovician, from the  
313 zone of minimum NPP reported previously at 30° S to the highly productive Panthalassic circumpolar  
314 current. On the contrary, Baltica underwent a migration from nutrient-rich mid-latitude waters in the  
315 Southern Hemisphere at 480 Ma to the depleted water masses centred on 30° S at 440 Ma.

316

## 317 **Discussion**

318 Here we compare our modelling results with the Ordovician geological record in order to validate our  
319 simulations. We also discuss some enigmatic biotic events in the light of our model runs, such as the  
320 sudden and widespread bioherm development that punctuated the Late Ordovician of Baltoscandia.

### 321 **Geological evidence for upwelling systems**

322 During the Ordovician two key coastal areas are typified by high levels of primary productivity in the  
323 model: the west coasts of Laurentia and tropical Gondwana (Fig. 1), in particular Australia and South  
324 China. These modelling results are supported by geological data. Indeed, a wide range of  
325 sedimentary indicators has been confirmed for a prolonged phase of upwelling across much of  
326 Laurentia during the Middle and Late Ordovician related to glaciation (Pope & Steffen 2003). A  
327 careful reassessment of the ages of many of the units (Leslie & Bergström 2003) indicates that the  
328 formation of cherts may be much more widespread, suggesting the possibility that this is related to  
329 more general phases of upwelling across the Laurentian continent. Associated biotic indicators are  
330 sparse and under-developed. Graptolites, however, were most common in upwelling zones along

331 continental margins. In the Vinini Formation, Roberts Mountains, Nevada, for example, changes  
332 within the graptolite zooplankton have been associated with fluctuating oceanographic conditions  
333 and the upwelling of anoxic waters. During high-stands graptolite faunas diversified within the OMZ  
334 but the ecosystem collapsed with the substantial fall of sea level associated with the end Ordovician  
335 glaciation and the retreat of the OMZ (Finney *et al.* 2007). Elsewhere in the Great Basin the macro-  
336 shelly fauna is abundant throughout much of the Ordovician, forming locally shell beds and  
337 concentrations (Finnegan & Droser 2005), with individuals increasing in size (Payne & Finnegan 2006)  
338 and shell thickness (Pruss *et al.* 2010); the faunas are never highly diverse but they are abundant.  
339 Bryozoan-rich deposits, formed by another suspension feeder, have also been associated with the  
340 upwelling of nutrients in parts of Laurentia during the later Ordovician (Taylor & Sendino 2010).

341 In detail the location of the large-scale upwelling systems simulated in the model is in relatively good  
342 agreement with most of the evidence of upwelling (cherts and phosphate deposits) documented by  
343 Pope & Steffen (2003) (Fig. 1A). Best match is observed on the western margin of the tropical  
344 landmasses, i.e., Laurentia and Gondwana. Some data points are more difficult to explain (e.g., in  
345 southeastern Laurentia), and the most outstanding model-data mismatch is observed in Baltica.  
346 Clearly, our simulation provides no explanation for the preservation of cherts in that precise location.  
347 In order to explain the discrepancy, we emphasize that the spatial resolution of our model (ca. 300  
348 km) does not allow us to capture small-scale processes. In addition, the land-sea mask interpolated  
349 on the model's grid constitutes a crude approximation of Ordovician coastlines. Finally, current  
350 palaeogeographical reconstructions only provide first-order indications of Early Palaeozoic  
351 bathymetry and topography and they generate large uncertainties in the position of the continental  
352 masses (up to 15° in latitude) (Lees *et al.* 2002), which makes any straightforward model-data  
353 comparison challenging.

354 To explain the appearance of these unusual carbonates with abundant chert and phosphate, Pope &  
355 Steffen (2003) required the strengthening of the meridional overturning circulation and associated  
356 increased nutrient supply to the ocean surface in response to glacial onset during the late Middle  
357 Ordovician. Because similarly high levels of primary productivity are simulated on the western  
358 margin of Laurentia during each of the three studied time slices (Fig. 1A-C), with no ice sheet over  
359 the South Pole, our model suggests that such coastal upwelling may instead have been a persistent  
360 characteristic of Ordovician oceans. These results are supported by the reappraisal of the age of  
361 many of the deposits originally reported by Pope & Steffen (2003), a number of them being  
362 potentially Early Ordovician in age (Leslie & Bergström 2003). Together this raises serious doubts  
363 about the climatic implications of the phosphatic rocks proposed by Pope & Steffen (2003). Glacial  
364 onset does not seem to be a necessary condition for strong upwelling to occur along the margin of

365 Laurentia.

366 Another possible indicator of high levels of primary productivity is the preservation of sediments  
367 enriched in organic matter. Melchin *et al.* (2013) published a compilation of Late Ordovician – early  
368 Silurian black shale occurrence. They illustrated three time slices immediately before, during and  
369 right after the Hirnantian glacial peak. Using simulations similar to ours, but focusing on the Late  
370 Ordovician, Pohl *et al.* (2017) recently demonstrated a striking correlation between the regions of  
371 high (low) primary productivity simulated in their model and the preservation of organic-rich  
372 (organic-poor) sediments in the geological record of the late Katian (i.e., the first time slice of  
373 Melchin *et al.* 2013). Similar to the cherts and phosphate deposits of Pope & Steffen (2003), the black  
374 shales are documented on the western margins of equatorial Laurentia and equatorial Gondwana,  
375 thus matching simulated upwelling systems (Fig. 1A). More interestingly, the deposits depleted in  
376 organic matter are found around Baltica and along the coast of Gondwana over the South Pole  
377 (Melchin *et al.* 2013), precisely where the model simulates local NPP minima (Fig. 1A). This model-  
378 data agreement supports the spatial patterns of NPP simulated in the present study. It also suggests  
379 that the preservation of black shales in the late Katian may have been driven by the patterns of  
380 primary production at the ocean surface (Pohl *et al.* 2017).

### 381 Baltoscandian reefs and mounds

382 In their comprehensive review, Kröger *et al.* (2016) demonstrated a critical change in the mode of  
383 carbonate production across the Baltic Basin during the latest Sandbian – earliest Katian (Late  
384 Ordovician, ca. 453 Ma). This boundary marked the beginning of a protracted period of widespread  
385 development of reefs in shallow-water areas and mud mounds in deeper epicontinental settings. The  
386 authors showed that biotic factors do not explain the initiation of Late Ordovician bioherm growth.  
387 They postulated climatic and eustatic drivers and further identified the northward drift of Baltica as  
388 the main determining factor for the timing of the start of the Baltic reef and mound development.  
389 More specifically, they suggested that '*the entry of Baltica in a geographical zone that allowed for a*  
390 *widespread bioherm formation was a major factor for the Sandbian radiation of reefal and reef-*  
391 *related organisms*'. Although the most direct effect of the latitudinal shift of Baltica was probably the  
392 establishment of climatic conditions more favourable to the shallow-water carbonate factory, our  
393 model runs also indicate that this northward migration made Baltica enter the nutrient-depleted  
394 tropical region during the Late Ordovician (Fig. 1A). Such unparalleled oligotrophic conditions may  
395 have provided the appropriate environmental background for the explosion of the bioherms on  
396 Baltoscandia.

397

## 398 **Limitations**

399 Our simulations provide an overview of possible spatial patterns of Ordovician NPP in time and space.  
400 However, it does not tell us anything about the total amount of NPP. The latter is a relatively direct  
401 function of nutrient availability in the ocean, which depends in turn on the intensity of continental  
402 weathering. Estimating continental weathering requires major assumptions on both the lithology and  
403 vegetation cover of emerged continental masses and global climate (e.g. Godd ris *et al.* 2014). In  
404 particular, weathering may have significantly varied throughout the Ordovician as a result of changes  
405 in global climate (Trotter *et al.* 2008), continental configuration (Nardin *et al.* 2011), volcanic activity  
406 (Lefebvre *et al.* 2010), land-ice cover (Pogge von Strandmann *et al.* 2017) or in response to the  
407 advent of the first land plants (Lenton *et al.* 2012; 2016; Porada *et al.* 2016). Such mechanisms do lie  
408 beyond what we are able to resolve using our ocean-atmosphere model. As a result, we are unable  
409 to predict the trend towards an increase or a decrease in NPP throughout the period.

410

## 411 **Conclusion**

412 Numerical simulations conducted with an ocean-atmosphere general circulation model with  
413 biogeochemical capabilities (MITgcm) predict the position and longevity of upwelling zones in the  
414 Ordovician Earth system. Upwelling zones host specific types of ecosystems, characterised by high  
415 organic productivity, abundant organisms (commonly opportunist species, often soft-bodied) but not  
416 necessarily high diversities. Nevertheless, high productivity levels may have provided the primary  
417 resources needed by superior consumers and thus paved the way for the development of more  
418 complex trophic chains featuring more diverse taxonomic assemblages. Fossil data have, to date, not  
419 been aligned with these predictions although accumulations of organic matter, bone and skeletal  
420 concentrations are identifiable in the fossil record and can be correlated with characteristic  
421 sediments, such as cherts, that signpost upwelling zones in deep time. The present study therefore  
422 targets in-depth analysis of the smaller members of the fossil record as the logical next step towards  
423 the integrated understanding of the diversification patterns throughout the early Palaeozoic.

424

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438

439

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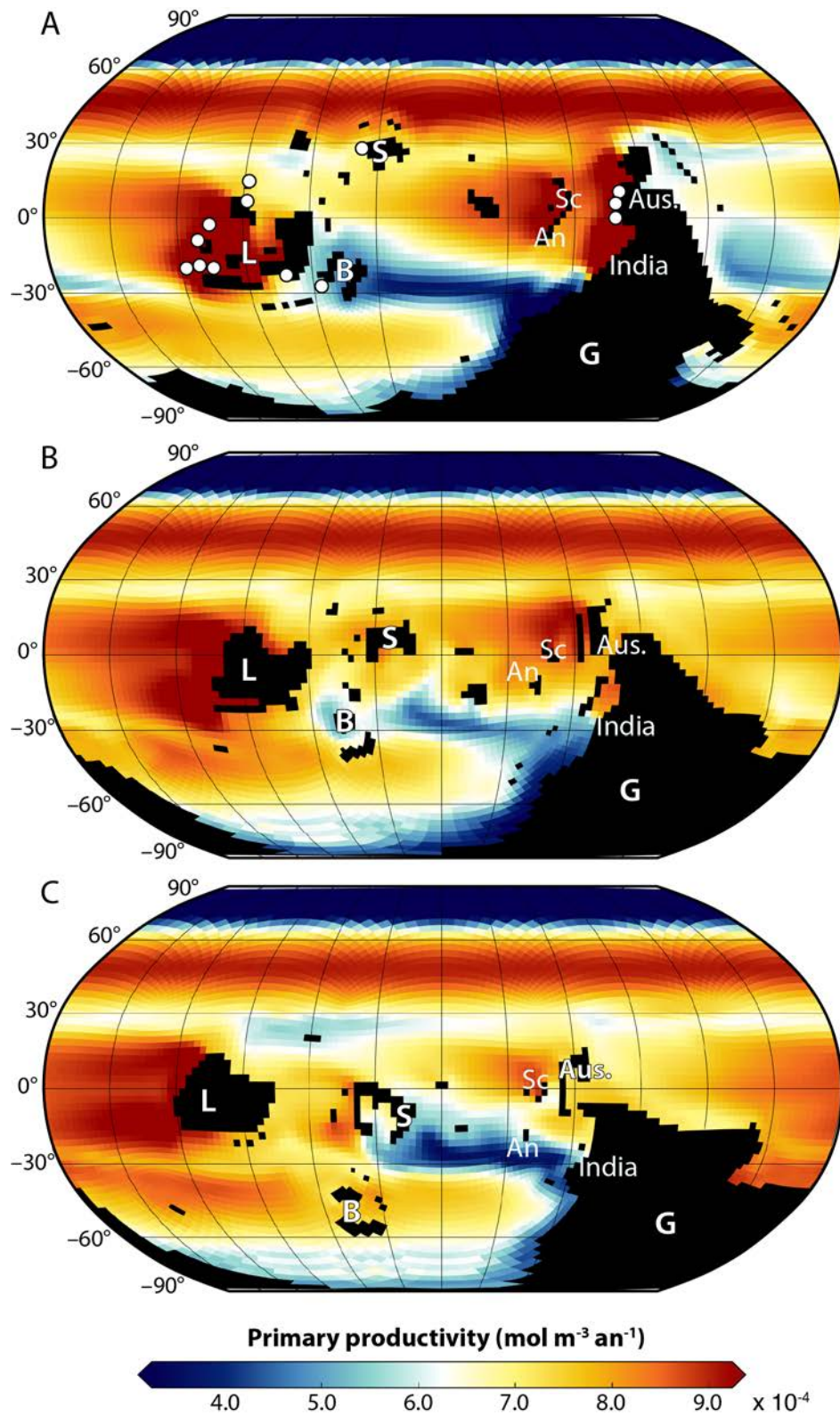
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**Figure 1:** Surface primary productivity simulated at 440 Ma (A), 460 Ma (B) and 480 Ma (C). The black mask indicates continental masses. In subfigure A, white points represent

evidence of upwelling. The latter are plotted on the Late Ordovician time slice following Pope & Steffen (2003), but see discussion in the main text. *L: Laurentia; B: Baltica; S: Siberia; G: Gondwana; Sc: South China; An: Annamia; Aus: Australia.*