

Author's response

**“BPOP-v1 model: exploring the impact of changes in the biological pump on the shelf sea and ocean nutrient and redox state”**

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Dear Editor,

Thank you very much for taking our manuscript into consideration for publication on GMD. We have carefully revised our manuscript following your and the Referees' suggestions, and include our extended answers in the following pages. We summarize here our main changes.

In line with the suggestions of Referee nr.1, we have modified our benthic model including anaerobic remineralization and a modulation of remineralization and burial rates as a function of oxygen. Following the suggestion of Referee nr.2, we have switched off the advection of Porg in the model. We have also included two further diagnostic variables, to easily check mass conservation. Overall, none of the modifications to the model has drastically changed the model's behaviour, confirming the robustness of our results and conclusions. We have also run a sensitivity experiment, discussed in the answer to Referee nr.2.

We have carefully revised our manuscript according to the changes to the model, extended the model evaluation, and double-checked all of the equations and tables. We have added a figure showing the time evolution of the variables and added two further tables: one listing the variables and their dimensions and one summarizing the evaluation.

We include below our extended answers to all of the comments and questions, followed by a version of the manuscript with track changes.

We look forward to your response.

Sincerely,

Elisa Lovecchio

## Answer to Editor's Comments

We thank the Editor for his comments and suggestions, which we copy below (in blue), and explain in detail our related changes to the manuscript (in red) and model.

*EC 1) Evaluation of your model (page 7) might benefit from a table which compares each of the quantities to the corresponding observational estimate (e.g. see Table 2 of Yool & Tyrrell, GBC, 2002)*

In agreement with this suggestion, we have added an evaluation table (**Table 5** of the revised manuscript) with the updated results of our model evaluation after revisions. We have updated our comments on the model evaluation in the related section 3 of the manuscript.

The table reads as follows:

Quantity	Model	Modern values or estimates	Units	Source
<b>Total ocean P</b>	3200 - 3400	3100	TmolP	Watson et al. (2017)
<b>Total ocean O<sub>2</sub></b>	100 - 150	220 (deep ocean)	PmolO <sub>2</sub>	Slomp and Van Cappellen (2006)
<b>P<sup>ss</sup></b>	1.5 – 1.8	1 – 1.5	mmol m <sup>-3</sup>	Garcia et al. (2018b); Sarmiento and Gruber (2006)
<b>P<sup>ds</sup></b>	4.5 – 6	2.2	mmol m <sup>-3</sup>	Garcia et al. (2018b); Watson et al. (2017)
<b>P<sup>so</sup></b>	0.5 - 1	0.2 - 2	mmol m <sup>-3</sup>	Garcia et al. (2018b); Sarmiento and Gruber (2006)
<b>P<sup>do</sup></b>	2.7 - 3	1 - 3	mmol m <sup>-3</sup>	Garcia et al. (2018b); Sarmiento and Gruber (2006)
<b>O<sup>ss</sup></b>	273	200 - 350	mmol m <sup>-3</sup>	Garcia et al. (2018a)
<b>O<sup>ds</sup></b>	4 - 20	0-80	mmol m <sup>-3</sup>	Garcia et al. (2018a)
<b>O<sup>so</sup></b>	273	200 - 350	mmol m <sup>-3</sup>	Garcia et al. (2018a)
<b>O<sup>do</sup></b>	75 - 120	40-200	mmol m <sup>-3</sup>	Garcia et al. (2018a)
<b>Production (Prod)</b>	1400 - 3000	3300 - 9000	TmolC yr <sup>-1</sup>	Carr et al. (2006)
<b>Export</b>	300 - 430	415 – 1660	TmolC yr <sup>-1</sup>	Henson et al. (2011)
<b>Export production</b>	10 % - 32 %	2 % - 20 %	of total Prod	Boyd and Trull (2007)
<b>Burial</b>	0.3 % - 0.7 %	0.4 %	of total Prod	Sarmiento and Gruber (2006)
<b>Shelf sea production</b>	12 % - 20 %	20 %	of total Prod	Barrón and Duarte (2015); Wollast (1998)
<b>Shelf sea export</b>	20 % - 23 %	29 %	of total Export	Sarmiento and Gruber (2006)
<b>Shelf sea burial</b>	100 %	91 %	of total Burial	Sarmiento and Gruber (2006)

**Table 5: Summary of the model evaluation provided in section 3. Modern observations and estimates are compared to model results obtained for  $z_{rem}^L$  in the range of measured values for a modern shelf sea (Cavan et al., 2017).**

*EC 2) I'm a little surprised that you haven't tuned your productivity to more realistic values, and that you lay the blame for your model's low productivity on its implicit microbial loop and missing distinction of new / regenerated production; it should be possible to achieve more realistic levels of productivity through tuning, and other models (again, Yool & Tyrrell, 2002) have no such difficulties while having the same limitations*

Following the modifications to the model's equations in agreement with the suggestions of Referee nr.1 and Referee nr.2, we have further retuned the model towards more realistic values of production and export. This was done by slightly modifying a few biogeochemical parameters (coagulation rate, Ca-P formation rate) and one physical parameter (vertical mixing in the shelf) in the range of plausible values. Further changes to the model, following recent literature, consisted in distinguishing between a water column and a sediment half saturation constant for aerobic remineralization. The combination of these changes in the equations and in a few parameter values allowed us to increase production and export (bringing them closer to the lower end of modern estimates), while still maintaining the values of export production and burial to export ratio in the range of current estimates. We modified the discussion of the model evaluation (subsection 3.2) accordingly.

*EC 3&4) Although you mention the timescales over which your model can easily be run (as well as alluding to simulating it across the Phanerozoic), none of your figures show the time evolution of your model; it might be informative for readers were you to include some indication of the model's time-evolution from, say, the arbitrary initial conditions that you list in Table 2 (e.g. see Figure 5 of Yool & Tyrrell, 2002)  
On a related point, how does your model compare in terms of residence times of the elements it represents?; given that it includes river inputs of P and reasonably represents ocean concentrations, I would expect it to do a good job here, but it might still be worth drawing attention to this*

To address this comment, we have included in the manuscript an additional figure (revised paper's **Figure 3**) to show an example of modelled tracer evolution. Furthermore, we have divided the Evaluation section in two parts with an initial subsection 3.1 focusing on the model dynamics and a second subsection 3.2 focusing on the comparison to model ocean budgets and fluxes (which corresponds to the old Evaluation before revisions).

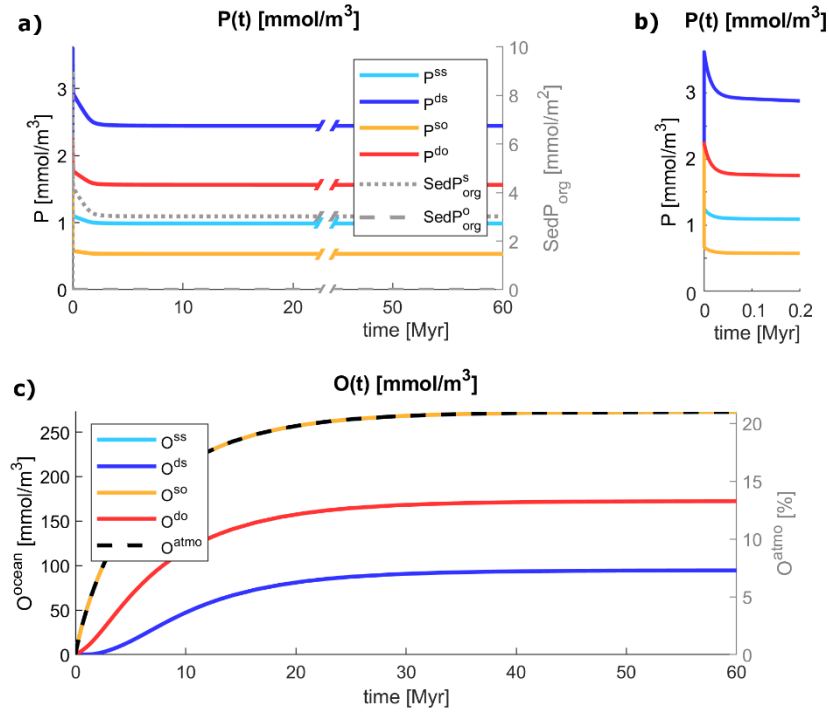
Subsection 3.1 of the revised manuscript reads as follows:

### **3.1 Timescales**

Starting from the initial values listed in Table 3, the modelled state variables evolve towards equilibrium for any couple of values of  $z_{rem}^S$  and  $z_{rem}^L$  in the explored interval. Simple mass conservation checks show no hidden source or sink of tracers in the model's boxes. Figure 3 illustrates an example of evolution of the variables for  $z_{rem}^S$  and  $z_{rem}^L$  in the middle of the interval of explored values for both particle types. In all the ocean boxes, P shows an initial oscillation that evolves on timescales of tens of thousands of years (Figure 3a,b), as expected by the typical timescale of evolution of the tracer (Lenton and Watson, 2000). This is followed by a slower drift which depends on the dynamics of the deep water oxygen content, as the release and burial of P in the sediments depends on the level of oxygenation of the deep ocean and especially of the deep shelf sea. P reaches complete equilibrium as soon as the deep ocean boxes become stably oxygenated. The timescales of evolution of O are slower and lay on the order of tens of millions of

years (Lenton and Watson, 2000). Oxygen in the deep shelf overcomes hypoxia after the first few millions of years and then slowly evolves towards equilibrium on the same timescale of O in the other ocean boxes. The dynamics of SedP<sub>org</sub> is also strongly driven by level of oxygenation of the deep shelf sea.

Figure 3 of the revised manuscript is shown below:



**Figure 3:** Evolution of the state variables from the initial conditions listed in Table 2 and remineralization lengths roughly in the middle of the interval of explored values:  $z_{rem}^S = 20$  m,  $z_{rem}^L = 250$  m. (a) Evolution of inorganic phosphorus  $P$  in the water column (left axis) and of organic phosphorus in the sediments  $SedP_{org}$  (right axis); (b) zoom on the dynamics of  $P$  in the two hundred thousand years; (c) Evolution of oxygen in the water column (left axis) and atmosphere (right axis). In subplot (c) the two lines  $O^{ss}$  and  $O^{so}$  are overlapping: the two variables evolve closely due to the coupling of the surface ocean with the atmosphere via air-sea gas exchange.

# BPOP-v1 model: exploring the impact of changes in the biological pump on the shelf sea and ocean nutrient and redox state

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**Abstract.** The ocean's biological pump has changed over Earth history from one dominated by prokaryotes, to one involving a mixture of prokaryotes and eukaryotes with trophic structure. Changes in the biological pump are in turn hypothesised to have caused important changes in the ocean's nutrient and redox properties. To explore these hypotheses, we present here a new box model including oxygen (O), phosphorus (P) and a dynamical biological pump. Our Biological Pump, Oxygen and Phosphorus (BPOP) model accounts for two – small and large – organic matter species generated by production and coagulation, respectively. Export and burial of these particles are regulated by a remineralization length ( $z_{\text{rem}}$ ) scheme. We independently vary  $z_{\text{rem}}$  of small and large particles in order to study how changes in sinking speeds and remineralization rates affect the major biogeochemical fluxes, and O and P ocean concentrations. Modelled O and P budgets and fluxes ~~lie reasonably~~ close to present estimates for  $z_{\text{rem}}$  in the range of currently measured values. Our results highlight that relatively small changes in  $z_{\text{rem}}$  of the large particles can have important impacts on the O and P ocean availability and support the idea that an early ocean dominated by small particles was nutrient rich due to inefficient removal to sediments. The results also ~~highlight-suggest~~ that ~~extremely low oxygen concentrations in the shelf~~ ~~shelf ocean~~ ~~anoxia~~ can coexist with an oxygenated deep open ocean for realistic values of  $z_{\text{rem}}$ , especially for large values of the small particle  $z_{\text{rem}}$ . This could challenge conventional interpretations that the Proterozoic deep ocean was anoxic, which ~~are-are~~ derived from shelf and slope sediment redox data. This simple and computationally inexpensive model is a promising tool to investigate the impact of changes in the organic matter sinking and remineralization rates as well as changes in physical processes coupled to the biological pump in a variety of case studies.

## 1 Introduction

The 'biological pump' describes the production of organic matter at the ocean's surface (an oxygen source), its downward export/sinking flux, remineralisation at depth (an oxygen sink), and burial. This set of processes acts against the homogenization of tracer concentrations by the ocean's circulation, maintaining large-scale tracer gradients (Sarmiento and Gruber, 2006). In today's world, the biological pump plays a key role in transferring carbon from the atmosphere/surface ocean to the deep ocean and in so doing lowers atmospheric  $\text{CO}_2$  and creates oxygen demand in deeper waters (Lam et al., 2011; Kwon et al., 2009). Those deeper waters with the greatest oxygen demand relative to oxygen supply can be driven hypoxic ( $\text{O}_2 < 60 \text{ mmol m}^{-3}$ ), suboxic ( $\text{O}_2 < 5 \text{ mmol m}^{-3}$ ) or even anoxic – as is being seen in parts of the ocean today (Keeling et al., 2010). By combining surface oxygen production and organic carbon burial, the biological pump plays a role in determining the long-term source of

oxygen to the atmosphere. The biological pump also provides a means of efficiently transferring organic matter and the nutrients it contains to marine sediments, if sinking through the water column happens fast enough compared to remineralization for the material to hit the bottom (Sarmiento and Gruber, 2006). Hence the biological pump plays a key part in balancing the input of phosphorus to the ocean with a corresponding output flux of phosphorus buried in marine sediments.

Through Earth's history, the characteristics, efficiency and impact of the biological pump are thought to have changed dramatically due to the evolution of increasingly large and complex marine organisms (Ridgwell, 2011; Logan et al., 1995; Boyle et al., 2018). Life in the ocean began as just prokaryotes, presumably attacked by viruses, with slow sinking of the resulting tiny particles. Now the marine ecosystem is a mix of prokaryotic cyanobacteria and heterotrophs, and size-structured eukaryotic algae, mixotrophs and heterotrophs all the way up to large jellyfish, fish and whales. Some of the resulting particles sink very fast (McDonnell and Buesseler, 2010). How changes in the biological pump have affected ocean nutrient and redox state at different times in Earth history is a subject of active research and hypothesis generation. Previous work has highlighted the Neoproterozoic Era, spanning from 1,000 to 541 million years ago, as of particular interest because it saw a shift of dominance from prokaryotes to eukaryotes and a series of dramatic shifts in the climate, biogeochemical cycling and ocean redox state (Katz et al., 2007; Brocks et al., 2017). A common paradigm has been to assume that a progressive rise of oxygen in the atmosphere (of uncertain cause) drove the oxygenation of the deep ocean at this time through air-sea gas exchange and mixing, but equally increases in the efficiency of the biological pump could have lowered ocean phosphorus concentration and thus oxygenated the ocean (Lenton et al., 2014). Recent data show a series of transient ocean oxygenation events ~660-520 Ma, which get more frequent over time, suggesting a complex interplay of processes on multiple timescales, including changes in the biological pump and ocean phosphorus inventory (Lenton and Daines, 2018).

During the Phanerozoic Eon there have been further changes to the biological pump. In particular, a rise of eukaryotic algae from the early Jurassic onwards is hypothesised to have increased the efficiency of the biological pump and thus oxygenated shallow waters (Lu et al., 2018), but presumably deoxygenated deeper waters, at least in the short term. In the oceanic anoxic events (OAEs) that occurred during the Mesozoic Era there were major increases in prokaryotic nitrogen fixation yet evidence for a eukaryote-dominated biological pump (Higgins et al., 2012), raising interesting questions as to whether this reinforced anoxia at depth.

Previous modelling work has examined the impact of changes in the organic matter remineralisation length/depth ( $z_{rem}$ ) in the 3D GENIE intermediate complexity model (Meyer et al., 2016; Lu et al., 2018). Both studies clearly demonstrated the important control of the  $z_{rem}$  on ocean oxygen concentrations – as it gets larger the oxygen minimum zone shifts to greater depths. Furthermore, Lu et al. (2018) showed that an increase in  $z_{rem}$  can explain an observed deepening of the oxycline from the Paleozoic to Meso-Cenozoic in the ocean redox proxy I/Ca. However, coarse 3D models such as GENIE do not really resolve shelf seas and their dynamics, which are distinct from those of the open ocean. Furthermore, GENIE only accounts for one organic carbon species, overlooking processes of transformation of organic material, such as coagulation and fragmentation, which contribute to modulate the efficiency of the organic matter vertical export and burial (Wilson et al., 2008; Karakaş et al., 2009; Boyd and Trull, 2007).

In this study we take a more idealised approach, exploring how changes in the properties of the biological pump may have affected the shelf sea and open ocean nutrient and redox state using a new Biological Pump, Oxygen

and Phosphorus (BPOP) box model. This model combines a box representation of the marine O and P cycles with an intermediate complexity representation of the biological pump transformations, including two classes of particulate organic matter (POM). BPOP allows us to modify the properties of two POM pools, whose abundance is regulated by the processes of production and coagulation. We focus on changes in the characteristic depths at which the two POM pools are remineralized, i.e., the particle remineralization length scale ( $z_{rem}$ ), and study the resulting equilibrium budgets and fluxes. In the following sections we describe the model, we provide an evaluation of its performance in the context of modern observations and flux estimates, and finally present and discuss our model results.

## 2 Model description

Here we describe the Biological Pump, Oxygen and Phosphorus (BPOP) model. The model was implemented using Matlab and the equations are solved by the built-in ode15s solver. BPOP can easily run on a single core, integrating 50 million years of time in less than a minute on an ordinary machine, and is therefore computationally efficient. We refer to the user's manual (see the supplementary material) for further information on how to run the model.

### 2.1 Variables and circulation

The box model resolves explicitly for each relevant box the local concentrations of three types of tracers: molecular oxygen  $O_2$  (O), inorganic dissolved phosphorus (P) and sedimented organic phosphorus ( $SedP_{org}$ ). The total budgets of P and O, respectively  $P^{TOT}$  and  $O^{TOT}$ , are also independently integrated from the net sources and sinks of the two tracers over the entire model domain, for the purpose of checking mass conservation. The entire set of the model's state and diagnostic variables and their units are listed in Table 1. In the following subsections we describe the box model's geometry and discuss the physical and geochemical fluxes that drive the tracers' dynamics. Box properties are listed in Table 24, while the set of parameters adopted for the modelled physical and geochemical fluxes can be found in Table 32.

#### 2.1.1 Box properties and physical fluxes of inorganic tracers

The box model includes 4 ocean boxes, 1 atmospheric box and 2 sediment boxes (Figure 1a). The ocean and sediment boxes are equally split between shelf sea and open ocean, both including one surface ocean box and one deep ocean box.

O and P are exchanged between the 4 ocean boxes through advection and mixing, including an fundamental upwelling recirculation between shelf sea and open ocean (Wollast, 1998). For a generic tracer concentration  $C$  and in the  $i^{th}$  box, the physical exchange flux is represented by

$$AdvMix(C)^i = \sum_j MassFlux_{ij}/V^i \cdot (C_j - C_i) \quad (1)$$

For each surface box  $i$ , air-sea gas exchange allows O fluxes between the ocean and the atmosphere (at). The flux is positive when directed into the ocean and depends on the gas transfer velocity  $K_w$  and Henry's constant  $K_{Henry}$ , as in:

$$AirSea^i = K_w \cdot (O^{at}/K_{Henry} - O^i) \cdot A^i/V^i \quad (2)$$

where  $K_w$  is a function of the prescribed mean temperature  $T_{mean}$  and wind speed  $W_{speed}$  (Sarmiento and Gruber, 2006).

### 2.1.2 Initialization and boundary fluxes

The model is initialized with an even concentration of P ( $P_{ini}$ ) in all the ocean boxes, zero oxygen and zero sediment  $P_{org}$ . A constant input of P from rivers ( $P_{in}$ ) into the surface ocean replenishes the P ocean reservoir despite the burial flux (net sink of  $P_{org}$ ) into the sediments.  $P_{in}$  is in part delivered directly to the surface open ocean (Sharples et al., 2017). At equilibrium, the  $P_{org}$  burial flux ~~must~~ balances  $P_{in}$ . Oxidative weathering determined by atmospheric ~~oxygen~~  $O^{at}$  constitutes a net sink flux for O. The weathering flux depends on a constant a baseline flux  $W_0$  and it scales like the square root of the oxygen concentration normalised to present values  $O_{mix_0}$  (Lenton et al., 2018), following:

$$OxyWeath = W_0 \cdot \sqrt{O^{at}/O_{mix_0}} \quad (3)$$

## 2.2 Biological pump details

The modelled tracer cycles are coupled by a set of biological transformations, i.e., the biological pump, governing the cycle of production, remineralization and burial of  $P_{org}$  in the water column and in the sediments.  $P_{org}$  in the water column is resolved implicitly: at each time step all the produced  $P_{org}$  that does not reach the sediments is instantaneously remineralized. In this sense, in our model no  $P_{org}$  can accumulate in the ocean's water column. This scheme is like the one used to represent detrital POM in some modern ocean biogeochemical models (Moore et al., 2004). P and O biological fluxes are coupled by a fixed Redfield ratio  $OP_{Red}$ . The next few paragraphs describe the cycle of production, coagulation, export, remineralization and burial that constitute the biological pump representation. The full set of parameters used to resolve the  $P_{org}$  cycle is provided in Table 43.

### 2.2.1 Particle classes, production and coagulation

The model includes two  $P_{org}$  classes which get produced, exported and remineralized in the ocean's water column: small  $P_{org}$  ( $SP_{org}$ ) and large  $P_{org}$  ( $LP_{org}$ ). The use of two  $P_{org}$  classes is in line with modern ocean in situ observations, which reveal a bimodal distribution of the particle sizes and sinking speeds (Riley et al., 2012; Alonso-González et al., 2010). Moreover, it allows to better reproduce the commonly observed Martin power-law decay of the particle export flux with the use of a remineralization length scheme of export and burial fluxes (Boyd and Trull, 2007).

Organic matter production happens only in the surface ocean boxes through the uptake of P. This is regulated by a maximum rate  $P_{eff}$  and a Michaelis-Menten kinetics with constant  $K_p$ . Production in each  $i^{th}$  box only generates  $SP_{org}$ , according to:

$$Prod^i = P_{eff} \cdot (P^i / (P^i + K_p)) \cdot P^i \quad (4)$$

$LP_{org}$  is generated via the coagulation of  $SP_{org}$  either at the surface after production or at depth after the export of  $SP_{org}$  from the surface. The coagulation of  $SP_{org}$  into  $LP_{org}$  in each box  $i$  is proportional to the square of the local  $SP_{org}$  concentration and is regulated by a coagulation rate  $cg_r$  (Boyd and Trull, 2007; Gruber et al., 2006), as in:

$$Coag^i = cg_r \cdot (SP_{org}^i)^2 \quad (5)$$

Coagulation impacts the relative contribution of small and large particles to the export and burial fluxes by subtracting from the local  $SP_{org}$  pool and adding to the  $LP_{org}$  pool.

## 2.2.2 Physical fluxes of organic material

The implicit representation of the organic matter in the water column implies that no organic matter is accumulated in the ocean. In our baseline version of the model, corresponding to the results presented in this manuscript,  $SP_{org}$  and  $LP_{org}$  are redistributed throughout the watercolumn exclusively by implicitly modelled gravitational sinking before being either buried, accumulated in the sediments or remineralized. Even though the ~~However, the model allows to include lateral advective and vertical mixing fluxes of organic phosphorus by setting to one the value of the parameter  $\gamma$ , which acts as a switch in the equations. This may be necessary when working with suspended  $SP_{org}$  pools ( $z_{rem}^S = 0$ ), and therefore that modelled  $SP_{org}$  and  $LP_{org}$  can only be transported by physical fluxes from regions of production to regions of remineralization. For this reason, physical fluxes affect the two organic matter species only in a single direction (Figure 1b). Despite this limitation, we believe that, as including the influence of these physical fluxes on the water column  $P_{org}$  is essential to account for both the vertical organic matter export by advective downwelling and mixing (Stukel and Ducklow, 2017), and the lateral organic matter redistribution from the coast to the open waters both at the surface and at depth (Lovecchio et al., 2017; Inthorn et al., 2006), may be important when working with suspended  $SP_{org}$  ( $z_{rem}^S = 0$ ), these fluxes are not currently accounted for in the model. When advected and mixed, implicitly modelled  $SP_{org}$  and  $LP_{org}$  can only be transported by physical fluxes from regions of production to regions of remineralization. For this reason, if included, these fluxes affect the two organic matter species only in a single direction (Figure 1b). Due to the wide extension of the modelled ocean boxes, lateral fluxes are assumed to only affect  $SP_{org}$ . The lateral export of  $SP_{org}$  reduces its availability for export and burial in the shelf sea, i.e., at each time step lateral fluxes out of the shelf happen before the  $SP_{org}$  vertical export and sedimentation fluxes are calculated.~~

## 2.2.3 Remineralization length scheme

The export and sedimentation fluxes of  $P_{org}$  through the water column are represented by a remineralization length scheme. In this representation, the vertical fluxes of organic matter  $f(z)$  vary exponentially with depth. The shape of the exponential depends on the value of the remineralization length ( $z_{rem}$ ) of each organic matter species:

$$f^k(z) = f_0^k \cdot e^{-\frac{z-z_0}{z_{rem}^k}}, \quad (6)$$

where  $f_0^k$  is the flux at the reference depth  $z_0$ , and the index  $k$  indicates the organic matter pool of reference, either small (S) or large (L). This representation of the export flux is convenient, as it does not depend on the specific choice of  $z_0$  (Boyd and Trull, 2007).

The remineralization length  $z_{rem}$  indicates the distance through which the particle flux becomes 1/e times (about 36 %) the flux at the reference depth (Buesseler and Boyd, 2009; Marsay et al., 2015). This quantity is expressed in metres and can be calculated as the ratio between the particle sinking speed and the particle's remineralization rate (Cavan et al., 2017). Consequently,  $z_{rem}$  implicitly contains information on several particle inherent properties (among which density, size, shape, organic matter liability) as well as information about the surrounding environment, e.g., the type of heterotrophs which feed upon the organic material (McDonnell and Buesseler, 2010; Baker et al., 2017). For simplicity, we assume that the remineralization length of small and large particles does not vary between shelf sea and open ocean boxes. We examine the potential impact of this limitation in the discussion section of the paper.

## 2.2.4 Sediments and burial

SP<sub>org</sub> and LP<sub>org</sub> accumulate in the sediments as SedP<sub>org</sub>, which is calculated as a density per unit of area. The sediment flux into the sediment box  $i$  depends on the organic matter concentration in the overlaying deep ocean box  $j$  and on the remineralization length of the two pools as in:

$$5 \quad \text{SedFlx}^i = (\text{SP}_{org}^j \cdot \exp(-\Delta Z_j / z_{rem}^S) + \text{LP}_{org}^j \cdot \exp(-\Delta Z_j / z_{rem}^L)) \cdot \Delta Z_j \quad (7)$$

The accumulated SedP<sub>org</sub> is partially slowly remineralized and partially irreversibly buried in a mineral form. Phosphorus burial as mineral Ca-P- is modelled as a function of the square of SedP<sub>org</sub> that accumulates in the sediments, in a way that is analogous to the dynamics of particle coagulation, and is regulated by a constant rate coefficient CaP<sub>r</sub>. Ca-P formation happens at a lower rate under low oxygen conditions (CaP<sub>r</sub><sup>\*</sup> = CaP<sub>r</sub> · f<sub>san</sub> with f<sub>san</sub> < 1), in agreement with observations and previous models (Slomp and Van Cappellen, 2006). The transition from aerobic and anaerobic conditions is controlled by a Michaelis-Menten type of function of the oxygen concentration in the deep ocean box  $j$  overlaying the sediment box  $i$ . The oxic and anoxic terms sum to the total formation term as in:

$$15 \quad \text{CaPform}^i = (\text{SedP}_{org}^i)^2 \cdot [\text{CaP}_r \cdot O^j / (O^j + K_O^S) + (\text{CaP}_r \cdot f_{san}) \cdot (1 - O^j / (O^j + K_O^S))] \cdot \text{CaP}_r \cdot \frac{(\text{SedP}_{org}^i)^2}{\text{CaP}_r} \quad (8)$$

This flux is essential to balance the continuous P river input, therefore preventing the ocean from overflowing with nutrients.

## 2.2.5 Remineralization in the water column and sediments

At each time step, remineralization in the water column completely depletes the P<sub>org</sub> that has not reached the sediments. In the two surface boxes, remineralization of P<sub>org</sub> that is not exported below the euphotic layer uses up part of the oxygen that was released by production. For this reason, net oxygen production in each surface box is proportional to the export of P<sub>org</sub> below the euphotic layer. Export from a surface box  $i$  to a deep box  $j$  happens both via gravitational sinking and via mixing, as in:

$$25 \quad \begin{aligned} \text{VExp}^i &= \text{SP}_{org}^i \cdot \exp(-(\Delta Z_{eu}/2) / z_{rem}^S) + \text{LP}_{org}^i \cdot \exp(-(\Delta Z_{eu}/2) / z_{rem}^L) \quad (9) \\ \text{VExp}^i &= \text{SP}_{org}^i \cdot \exp(-(\Delta Z_{eu}/2) / z_{rem}^S) + \text{LP}_{org}^i \cdot \exp(-(\Delta Z_{eu}/2) / z_{rem}^L) + \\ &\quad \frac{(\text{SP}_{org}^i + \text{LP}_{org}^i) \cdot \text{Mix}_{ij}}{V^i} \quad (9) \end{aligned}$$

At depth, the remineralization of P<sub>org</sub> that does not reach the sediments happens through both aerobic and anaerobic processes, completely depleting the remaining P<sub>org</sub>. Water-column remineralization of P<sub>org</sub> into inorganic P in the deep box  $j$  is therefore calculated as:

$$30 \quad \text{WcRem}^j = \text{SP}_{org}^j \cdot (1 - \exp(-\Delta Z_j / z_{rem}^S)) + \text{LP}_{org}^j \cdot (1 - \exp(-\Delta Z_j / z_{rem}^L)) \quad (10)$$

In each deep ocean box  $i$ , aerobic remineralization uses some of the available oxygen and is therefore limited by a Michaelis-Menten kinetics with a half-saturation constant K<sup>w</sup><sub>O</sub> (DeVries and Weber, 2017). —Anaerobic remineralization takes up the entire remaining P<sub>org</sub> that is not remineralized aerobically and releases a product which “bubbles up” to the atmosphere, reacting with atmospheric oxygen.

35 In each sediment box  $i$ , aerobic-remineralization of SedP<sub>org</sub> happens in a similar way to remineralization in the water column, with an aerobic and an anaerobic component. However, remineralization in the sediments is not instantaneous, but happens at a fixed rate which depends on the oxygenation state of the overlaying water column. Aerobic remineralization takes up oxygen from the overlaying deep-water box  $j$  and happens at a ~~constant~~ rate

~~rm<sub>r</sub>, while being which is~~ limited by a Michaelis-Menten coefficient, ~~analogously to aerobic remineralization in the deep water column. Anaerobic remineralization releases its product to the atmosphere and happens at a faster rate~~  $rm_r^* = rm_r \cdot fe_{an}$  with  $fe_{an} > 1$ , in agreement with recent observations and previous models (Slomp and Van Cappellen, 2006). ~~Total sediment remineralization is therefore the sum of the two terms as in~~ This flux is regulated by a constant remineralization rate coefficient  $rm_r$  as in:

$$SedRem^i = rm_r \cdot SedP_{org}^i \cdot (O^j / (O^j + K_O^s K_T)) + (rm_r \cdot fe_{an}) \cdot SedP_{org}^i \cdot (1 - O^j / (O^j + K_O^s)) \quad (11)$$

## 2.3 Equations summary

The dynamics of the model's 11 state variables is regulated by just as many equations. We summarize here the major terms for P, O and SedP<sub>org</sub> in the surface ocean (s), deep ocean (d), atmosphere (at) and sediments, without distinguishing between coastal and open ocean boxes and assuming that all terms have been scaled with the reference box' dimensions. A full set of equations including the explicit formulation of all the flux terms for each box can be found in the paper's Appendix.

$$\frac{dP^s}{dt} = P_{in} + AdvMix(P)^s - VExp, \quad (12)$$

$$\frac{dP^d}{dt} = AdvMix(P)^d + WcRem + SedRem \quad (13)$$

$$\frac{dO^s}{dt} = AdvMix(O)^s + VExp \cdot OP_{Red} + AirSea \quad (14)$$

$$\frac{dO^d}{dt} = AdvMix(O)^d - WcRem_{Aer} \cdot OP_{Red} - SedRem_{Aer} \cdot OP_{Red} \quad (15)$$

$$\frac{dSedP_{org}}{dt} = SedFlx - CaPform - SedRem \quad (16)$$

$$\frac{dO^{at}}{dt} = -\sum AirSseaFlx - WcRem_{Ana} \cdot OP_{Red} - SedRem_{Ana} \cdot OP_{Red} - OxyWeath \quad (17)$$

Where: P<sub>in</sub> is the river input of P to the ocean's surface, AdvMix indicates the advective and mixing physical fluxes of the variable of interest (which differ for each box according to the circulation scheme); Exp is the export flux of P<sub>org</sub> in P units; WcRem indicates the water column complete remineralization of the organic material in P units, which is split into an anaerobic (Ana) and aerobic (Aer) component; SedRem indicates the sediment remineralization of SedP<sub>org</sub> in P units (also aerobic and anaerobic); AirSseaFlx represents the air-sea flux exchange of O; OxyWeath is the O weathering flux sink; SedFlx is the SedP<sub>org</sub> accumulation flux as regulated by the remineralization length scheme at the bottom of the water column; and finally CaPform represents the sediment burial flux of P in mineral form. For each box, flux terms are rescaled with the appropriate box geometry.

## 2.4 Strategy: sensitivity studies for varying $z_{rem}$

In order to characterize the model, we analyse the equilibrium budgets and fluxes of the state variables for varying  $z_{rem}$  values separately for  $SP_{org}$  and  $LP_{org}$ , respectively  $z_{rem}^S$  and  $z_{rem}^L$ . We adopt a range of  $z_{rem}$  values that fall close to modern observations (Cavan et al., 2017; Buesseler and Boyd, 2009; Marsay et al., 2015) and keeps into consideration our future aim to apply the model to simulate the impact of the time evolution of the early biological pump (at the Neoproterozoic-Palaeozoic transition). For this reason, we don't push the range as far as what would be needed to consider the impact of fast sinking rates typical of silicified or calcified small phytoplankton (McDonnell and Buesseler, 2010; Lam et al., 2011). In our sensitivity simulations,  $z_{rem}^S$  is in the range of [0, 40 m], while  $z_{rem}^L$  varies in the range of [50 m, 450 m].

## 3 Evaluation

### 3.1 Timescales

Starting from the initial values listed in Table 3, the modelled state variables evolve towards equilibrium for any couple of values of  $z_{rem}^S$  and  $z_{rem}^L$  in the explored interval. Simple mass conservation checks show no hidden source or sink of tracers in the model's boxes. Figure 3 illustrates an example of evolution of the variables for  $z_{rem}^S$  and  $z_{rem}^L$  in the middle of the interval of explored values for both particle types. In all the ocean boxes, P shows an initial oscillation that evolves on timescales of tens of thousands of years (Figure 3a,b), as expected by the typical timescale of evolution of the tracer (Lenton and Watson, 2000). This is followed by a slower drift which depends on the dynamics of the deep water oxygen content, as the release and burial of P in the sediments depends on the level of oxygenation of the deep ocean and especially of the deep shelf sea. P reaches complete equilibrium as soon as the deep ocean boxes become stably oxygenated. The timescales of evolution of O are slower and lay on the order of tens of millions of years (Lenton and Watson, 2000). Oxygen in the deep shelf overcomes hypoxia after the first few millions of years and then slowly evolves towards equilibrium on the same timescale of O in the other ocean boxes. The dynamics of SedPorg is also strongly driven by level of oxygenation of the deep shelf sea.

### 3.2 Modern ocean budgets and fluxes

Modern estimates of the  $z_{rem}^S$  and  $z_{rem}^L$  vary depending on the region of sampling and on the local community structure, with most of the measurements focusing on large or heavy particles and most studies focusing on the open ocean (Iversen and Ploug, 2010; Cavan et al., 2017; Lam et al., 2011). Furthermore, only a very limited number of measurements accounts for both microbial and zooplankton remineralization, the latter disregarded by lab measurements of  $z_{rem}$  (Cavan et al., 2017). Considering the fundamental role of the shelf sea in our model (always accounting for > 98 % of the total burial), we evaluate modelled tracer budgets and fluxes for values of  $z_{rem}^L$  that lay around 76 m, as measured in situ by Cavan et al. (2017) for a modern shelf sea. We pose no restrictions on  $z_{rem}^S$  due to the lack of precise measurements. A summary of our evaluation is provided in Table 5.

In the this above mentioned range of  $z_{rem}$ , model results are lower but in the same order of magnitude of current estimates for marine tracer budgets (Figure 3). Our model predicts equilibrium budgets of about between 2500-3200 TmolP and 3400 TmolP for phosphorus, and an oxygen budget of between 100 PmolO<sub>2</sub> and 150 PmolO<sub>2</sub>

in the entire ocean, compared to the estimated total P reservoir of 3100 TmolP (Watson et al., 2017) and estimated deep ocean O<sub>2</sub> reservoir of 220 PmolO<sub>2</sub> (Slomp and Van Cappellen, 2006). Due to the relative size of the ocean boxes, it is important to underline that total budgets are strongly driven by the deep open ocean budget.

Deep shelf P and O concentrations lay in the ranges of [~~4.53~~ 5 mmol m<sup>-3</sup>, ~~64.5~~ mmol m<sup>-3</sup>] and [~~34~~ mmol m<sup>-3</sup>, ~~20~~ 5 mmol m<sup>-3</sup>] respectively (Figure ~~5.64,5~~). Deep shelf nutrient concentrations are higher than expected by a factor of two or three compared to modern values, possibly due to the fact that our model does not store any P<sub>org</sub> in the water column or due to an underestimation of the vertical supply of nutrients to the surface shelf (e.g., via mixing). Limiting deep P concentrations via lower remineralization or higher burial rates, however, also results in sensibly lower production rates. In the deep open ocean, P and O concentrations ~~fall in the ranges of shift to about 2.2~~ [~~2.7~~ mmol m<sup>-3</sup>, ~~3~~ mmol m<sup>-3</sup>] and ~~120~~ [~~75~~ mmol m<sup>-3</sup>, ~~125~~ mmol m<sup>-3</sup>] respectively, ~~with minor changes for varying z<sub>rem</sub><sup>S</sup>.~~ For any combination of z<sub>rem</sub><sup>S</sup> and z<sub>rem</sub><sup>L</sup>, O levels in surface ocean boxes lay ~~around~~ between 273 mmol m<sup>-3</sup> and 272.5 mmol m<sup>-3</sup>, a good approximation of average modern surface values (Garcia et al., 2018a). In general, the deep shelf always shows the highest P values and lowest O concentrations compared to the other ocean regions, while, as expected, the surface shelf sea is richer in P compared to the surface open ocean.

Modelled biological fluxes, such as production and export and burial, fall around the low end lower but of the same order of magnitude of present estimates (Figure 76). This is possibly due to the elementary representation of production in our model, which does not account for explicitly for the influence of the microbial loop nor distinguishes between new and regenerated production. We find Our model predicts an equivalent C primary production of between ~~1000~~ 1400 TmolC yr<sup>-1</sup> and ~~1800~~ 3000 TmolC yr<sup>-1</sup>, and an export below the euphotic layer ranges between 300 TmolC yr<sup>-1</sup> and 430 TmolC yr<sup>-1</sup>, both calculated using a fixed C:P Redfield ratio of 106. ~~These~~ must be compared to an expected value of production of at least 3300 TmolC yr<sup>-1</sup>, ~~reaching up to more than 9000 TmolC yr<sup>-1</sup> according to satellite estimates~~ (Carr et al., 2006). ~~E and an estimated export flux below the euphotic layer ranges between 250 TmolC yr<sup>-1</sup> and 300 TmolC yr<sup>-1</sup>, compared to an estimated value that lays between of at least 415 TmolC yr<sup>-1</sup> and 1660 TmolC yr<sup>-1</sup> (Henson et al., 2011). Even though~~ Despite the absolute values of the fluxes ~~are being~~ lower than expected, modelled export production (the export to production ratio) and the burial to production ratio compare well to range of present estimates, the relative magnitude of the fluxes compared to production lay in the range of present estimates. The modelled export corresponds to between ~~15~~ 10 % and ~~35~~ 32 % of total production, strongly depending on z<sub>rem</sub><sup>S</sup>, compared to an expected range of 2 % - 20 % (Boyd and Trull, 2007). Buried P<sub>org</sub> corresponds to between 0.~~34~~ % and 0.~~78~~ % of total production, compared to an expected 0.4 % (Sarmiento and Gruber, 2006).

In terms of the shelf contribution to the total fluxes, model results also fall close to present estimates. Modelled production in the surface shelf sea represents between ~~14~~ 12 % and 20 % of total production (expected 20 %) (Barrón and Duarte, 2015; Wollast, 1998). The fraction of modelled export and burial that happens in the shelf region represent, respectively, ~~about~~ [~~20~~ %, ~~23~~ %] and nearly 100 % of the total ocean fluxes, compared to estimated modern values of 29 % and 91 % (Sarmiento and Gruber, 2006). Our overestimation of the shelf contribution to the burial fluxes may be due to the underestimation of the open ocean particles z<sub>rem</sub> compared to observations (Cavan et al., 2017; Lam et al., 2011), i.e. due to our choice of using the same value of z<sub>rem</sub><sup>S</sup> and z<sub>rem</sub><sup>L</sup> for both the coastal and the open ocean box. This simplifying assumption limits the capacity of P<sub>org</sub> to reach the deep sediment layer in the open ocean. We explore potential limitations of this choice in the Discussion section.

## 4 Results

### 4.1 Budgets and fluxes sensitivity to changes in $z_{rem}$

Around the lowest values of  $z_{rem}^L$  adopted in the present study, i.e., in the range of [50 m, 100 m], our model shows a strong sensitivity of the total and local ocean P and O budgets for small changes of  $z_{rem}^L$  (Figure 43). This is true for any  $z_{rem}^S$ , with minor differences between low and high  $z_{rem}^S$  values. For smaller  $z_{rem}^L$ , the model shows a sharp increase in P concentrations in all the ocean boxes and a substantial decrease of O levels at depth (Figures 5.64,5), which are coupled to high levels of production and remineralization and low rates of sedimentation (Figure 76). Essentially slow sinking and/or rapid remineralization results in inefficient removal of P to shelf sea sediments, requiring the ocean concentration of P to rise considerably for P output to balance (fixed) P input to the ocean.

Our model results show that for any couple of values of  $z_{rem}^S$  and  $z_{rem}^L$  in the entire explored range, the biological pump is able to oxygenate the surface ocean (surface O levels lay close to 2732 mmol m<sup>-3</sup>) and, for most values, also to maintain the deep ocean above the level of hypoxia (Figure 65). The model shows a substantial difference between the deep shelf and the deep open ocean: while the latter is substantially oxygenated (O > 50 mmol m<sup>-3</sup>) for nearly any value of  $z_{rem}^S$  and  $z_{rem}^L$ , the deep shelf is hypoxic or even suboxic for a broad range of small values of  $z_{rem}^L$ , especially close to modern shelf  $z_{rem}^L$  observations. Considering the wide spatial extension of our boxes, we expect these low oxygen levels to indicate the development of local anoxia in the deep shelf.

In a limited interval of small  $z_{rem}^S$  values (roughly  $z_{rem}^S < 6$  m), model results depend only on the LP<sub>org</sub> properties due to the rather irrelevant contribution of SP<sub>org</sub> to export and remineralization. For larger  $z_{rem}$  values ( $z_{rem}^S > 6$  m and  $z_{rem}^L > 100$  m), model results show a strong interdependence of equilibrium budgets and absolute fluxes on both  $z_{rem}^S$  and  $z_{rem}^L$ . Interestingly, in this range of values, ~~the ratio of export to~~ production depends nearly entirely on the small particle properties, ranging between 2010 % for low  $z_{rem}^S$  and 4032 % for high  $z_{rem}^S$ , an overall trend that affects also the ratio of deep remineralization to surface production (Figure 76).

It is also important to notice that, for any couple of  $z_{rem}^S$  and  $z_{rem}^L$ , modelled tracer concentrations and fluxes fall in a range of values that never exceeds by orders of magnitude the modern observed values. Considering all of the ocean boxes, P concentrations vary in the range of roughly 0.3 mmol m<sup>-3</sup> and 6.58 mmol m<sup>-3</sup>, while O levels lay between 1 mmol m<sup>-3</sup> and 200 mmol m<sup>-3</sup>. Production in carbon units lays in the interval [600800 TmolC yr<sup>-1</sup>, 22004100 TmolC yr<sup>-1</sup>].

### 4.2 Budgets and fluxes contribution by particle class

#### ~~The 4.2 Budgets and fluxes contribution by particle class~~

~~The~~ relative role of small and large particles to modelled biological and physical fluxes depends on a combination of their inherent properties ( $z_{rem}$ ) and of coagulation. Coagulation of SP<sub>org</sub> into LP<sub>org</sub> after production in surface boxes affects between 2013 % and 5055 % of the small particles in the surface shelf sea and between 54 % and 2528 % of the small particles in the surface open ocean (Figure 87a,b). The highest rates of coagulation of SP<sub>org</sub> into LP<sub>org</sub> in the surface ocean are found for especially high P concentrations resulting in high rates of small particle production. Rates decrease quickly moving away from these high P condition. These correspond to roughly  $z_{rem}^L < 100$  m, meaning rather labile or light large particles, which contribute poorly to P removal and net O production.

For  $z_{rem}^L > 100$  m,  $LP_{org}$  efficiently remove P from the water column, limiting production. Coagulation rates are therefore lower and vary in a more limited range of values. For this reason, the contribution of  $SP_{org}$  to the total export below the euphotic layer is strongly dominated by the value of  $z_{rem}^S$ , with a null contribution to export for all values of  $z_{rem}^S < 10$  m and increasing values above it. This trend is reflected in the deep-water small particle fraction (Figure 8c,d). Coagulation rates at depth, even though lower compared to the surface, still reach values of a few percent in the shelf sea ( $\leq 6$  % of the exported  $SP_{org}$ ). Small particles contribute ~~up to between 5 % and 5066~~ % to export and ~~up to between 5 % and 1525~~ % to the sediment accumulation in the shelf sea, with the highest contribution to sediment accumulation being reached for large  $z_{rem}^S$  and low  $z_{rem}^L$ . In the open ocean, small particles represent ~~up to between 30 % and 8087~~ % of the total export, with the percentage being strongly dependent on the value of  $z_{rem}^S$ . Our model highlights therefore the different role of large and small particles in the determination of the equilibrium budgets and fluxes. Coagulation into large (fast sinking, less liable) particles is essential to maintain high enough sedimentation and burial rates, therefore allowing O accumulation in the system. At the same time, small (slow sinking, more liable) particles tune the total magnitude of export and remineralization below the euphotic layer, impacting the distribution of oxygen and nutrients throughout the water column.

## 5 Discussion

### 5.1 Model limitations and robustness

#### 5.1.1 Box model limitations

BPOP consists in a simple box model with 4 ocean boxes, 2 sediment boxes and 1 atmospheric box. As with every box model, BPOP only allows a very rough and fundamental representation of the ocean's topography and circulation as well as of the exchange fluxes between ocean, atmosphere and sediments. Even though this may be a limitation in the context of the study of the well-known modern (and future) ocean, such a computationally inexpensive model can be a useful tool to for a first exploration of a large variety of projected conditions. In the context of understanding past ocean changes, often characterized by a limited availability of observational data, the use of such a simple model constitutes instead an effective and honest approach to understand global shifts in budgets and fluxes. Furthermore, BPOP explicitly distinguishes between the well sampled shelf sea and the less known open ocean of deep time, therefore allowing to relate shelf data with large scale open sea conditions.

#### 5.1.2 Limitations connected to the biological pump representation

In our model we adopt a very simplified representation of the biological pump, including two particle classes, “small” and “large”, generated by production and coagulation, assuming that, on average,  $z_{rem}^S < z_{rem}^L$ . This scheme resembles the one commonly used in ocean biogeochemical models (Gruber et al., 2006; Jackson and Burd, 2015). Our model does not include a DOM pool for reasons mostly connected to the implicit representation of the biological pump and the complete remineralization of the non-sedimented organic material at each integration step.

Modelled particles get remineralized through the water column according to their characteristic  $z_{rem}$ . Even though for simplicity we do not use a continuum spectrum of  $z_{rem}$ , the use of two particles classes is in line with

observations showing two distinct peaks in the observed distribution of particles' sinking speeds (Riley et al., 2012; Alonso-González et al., 2010). Furthermore, this simplification still allows to closely approximate the empirical particle flux curve as a function of depth, also known as Martin's curve (Boyd and Trull, 2007).

We assume that  $z_{rem}^S$  and  $z_{rem}^L$  do not vary between the shelf sea and the open ocean. However, modern ocean observations show cross-shore changes in the phytoplankton community structure and sinking speeds (Barton et al., 2013). Our simplifying assumption may therefore cause the overestimation of the relative contribution of the shelf sea to the total burial flux of  $P_{org}$ . Despite this, we believe that this choice is still convenient in the context of the current model, as it allows us to reduce the number of parameters in such a simple box model representation of the ocean's biological pump.

Observations suggest that hard shelled phytoplankton types, especially calcified cells, contribute substantially to the vertical export and burial of the organic material thanks to extremely large  $z_{rem}$  despite their small size (Lam et al., 2011; Iversen and Ploug, 2010). In the present study we focus on an interval of  $z_{rem}^S$  and  $z_{rem}^L$  values that are most likely to resemble the biological pump conditions of the Neoproterozoic - early Paleozoic ocean, before the evolution of such phytoplankton types. However, the model allows to explore different ranges of  $z_{rem}^S$  and  $z_{rem}^L$  values and to tune the rate of coagulation in order to explore the influence of these phytoplankton classes. Even though bacterial remineralization is thought to be the dominant pathway for organic matter recycling on a global scale, especially at low latitudes (Rivkin and Legendre, 2001), modern ocean coastal environments are also characterized by high grazing rates. The evolution of zooplankton and increasingly large grazers may have had a different impact on the effective  $z_{rem}^S$  and low  $z_{rem}^L$ , ~~giving due to~~ additional  $P_{org}$  transformations such as particle fragmentation due to sloppy feeding (Cavan et al., 2017; Iversen and Poulsen, 2007). These processes can limit the large particle burial rates, while resulting in the deep production of small particle, s-POM and DOM. Our model does not currently account for particle fragmentation, however the process could be easily considered in future model developments. In this context, new processes such as the sedimentation and burial of large grazers should also be considered.

### 5.1.3 Sensitivity to parameter choices

We discuss here the model sensitivity to changes in a set of significant parameters adopted to describe its geometry, circulation and biological processes. Overall, none of the sensitivity experiments showed significant changes in the model results and conclusions: trends in budgets and fluxes obtained varying  $z_{rem}^S$  and  $z_{rem}^L$ , as well as our main results regarding the relative deep shelf and open ocean oxygenation remain unchanged.

Among the geometrical box model parameters, a key value is represented by the percentage of shelf sea area ( $\mathcal{P}_{shelf}$ ). An increase (e.g., doubling) in  $\mathcal{P}_{shelf}$  results in an overall decrease in the total budget of  $P$  and increase in  $O$  due to the larger ratio of burial to production, which is facilitated by a larger extension of the surface of shallow water. Interestingly, deep shelf anoxia is enhanced for larger  $\mathcal{P}_{shelf}$ , i.e., anoxia is observed for a wider range of  $z_{rem}^S$  and  $z_{rem}^L$  values, while the deep ocean tends to be more oxygenated. Despite a doubling of  $\mathcal{P}_{shelf}$ , however, model results largely remain in the same range of those found for modern  $\mathcal{P}_{shelf}$ .

We explored the effect of varying the physical circulation parameters. Changes in upwelling (Upw), have an important impact on the modelled ocean's budgets. An increase in Upw induces a lowering of  $P$  levels, especially in the deep shelf, due to their recirculation towards the surface and consequent uptake by production. This is coupled to an overall larger equilibrium  $O$  budget due to higher storage in the deep open ocean, and consequent

recirculation into the deep shelf. Deep shelf ~~anoxia-suboxia~~ is still possible, but for a more limited range of  $z_{rem}^L$  values. Changes in vertical mixing in the open ocean ( $Mix_{vo}$ ) ~~do not seem to~~ affect the overall P and O budgets; ~~but they do impact O mostly for high  $z_{rem}^L$~~ . For lower  $Mix_{vo}$ , the O budget decreases due to lower O storage at depth, while P increases. Changes in vertical mixing on the shelf ( $Mix_{vs}$ ), instead, have a minor impact on the model's total budgets and fluxes, while locally modulating shelf oxygen and nutrient concentrations. Lateral mixing fluxes ( $Mix_{ls}$ ,  $Mix_{ld}$ ) were included in our model for means of generalization and in order to account for the influence of non-upwelling margins, with a lower value than in previous studies (Fennel et al., 2005). Changes in  $Mix_{ls}$  and  $Mix_{ld}$  result in significant changes in the deep ocean storage of tracers and on open ocean production, with little impact on the budget of the other ocean boxes. However, also in this case, our main conclusions remain unaffected.

We explored the impact of changing the portion of nutrients delivered directly to the open ocean,  $\mathcal{P}_{open}$ . Even large changes in this parameter do not significantly affect the model's results, indicating that the relative levels of P and O at equilibrium are determined by the internal physical and biogeochemical dynamics of the model, rather than by boundary conditions.

Lastly, we explored the model sensitivity to the choice of key biogeochemical parameters representing rates of transformation. Both the use of higher coagulation rates ( $cg_r$ ) and the use of higher ~~higher~~ rates of formation of mineral Ca-P ( $CaP_r$ ) result in a general increase in O levels and decrease in nutrient availability due to larger sedimentation and burial rates. However, we find again no substantial change in the model behaviour nor in the relative contribution to budgets and fluxes of each modelled ocean box.

## 5.2 Model applications

### 5.2.1 Past changes in the biological pump

The evolution of larger and heavier cells during the Neoproterozoic and across the Neoproterozoic-Paleozoic transition is hypothesised to have caused significant changes in the ocean's nutrient and redox state (Lenton and Daines, 2018). Our new model can be used to assess the impact of this evolution in both the shelf and the open ocean. Our first model results highlight that for small  $z_{rem}^L$ , i.e., for an early biological pump with reduced capacity of export and burial, nutrient levels and production rates are particularly high. At the same time, an increase in  $z_{rem}^S$  alone, fuelling higher remineralization rates at depth, can induce anoxia in the deep shelf while still maintaining the deep open ocean substantially oxygenated. The possibility of a coexistence of an anoxic deep shelf with an oxygenated deep open ocean has important implications for the interpretation of deep time redox proxy data, which come almost exclusively from shelf and slope environments, yet have been widely used to infer deep ocean anoxia for most of the Proterozoic Eon (Lenton and Daines, 2017). We plan to use our model to further explore these changes in a time-frame perspective, introducing time varying boundary conditions (such as changes in  $P_{in}$ ) and parameter properties.

Phytoplankton evolution as well as the development of heavier and larger marine organisms continued throughout the Phanerozoic (Katz et al., 2007). BPOP can also be used to explore the role of the biological pump in the onset of OAEs in the course of the Mesozoic era, likely induced by enhanced productivity due to an upwelling intensification (Higgins et al., 2012). During the Mesozoic era, the evolution of dinoflagellates, calcareous and silica-encased phytoplankton also likely impacted the export and burial rates in a significant way (Katz et al., 2004). By extending the range of explored values of  $z_{rem}^S$  and  $z_{rem}^L$ , or possibly including the effect of grazing

and/or an additional heavy POC class for shelled organisms, BPOP can also be used to study the consequences of such evolution.

### 5.2.2 Future changes in the biological pump

Predicted future changes connected to global warming include, among the others, changes in ocean temperature, pH and stratification (Gruber et al., 2004), with additional repercussions on plankton community structure, production, remineralization and export rates (Laufkötter et al., 2017; Acevedo-Trejos et al., 2014; Kwon et al., 2009). Our results show that around values of  $z_{\text{rem}}^L$  measured for modern shelf environment (Cavan et al., 2017) modelled equilibrium budgets and fluxes are very sensitive to small changes in  $z_{\text{rem}}$ . This indicates a potentially high sensitivity of the modern ocean to small changes in the biological pump, which may be particularly important in the deep shelf, where the boundary with ~~anoxia-suboxia~~ is especially close (Keeling et al., 2010). Our model can be used to get a first assessment of the large-scale combined effect of predicted changes in the biological pump with expected shifts in the physical ocean properties.

### 5.2.3 Exploring past and future changes in geometry, physics and biogeochemistry

In the present study we have focused on the impact of changes of  $z_{\text{rem}}^S$  and  $z_{\text{rem}}^L$  on the equilibrium budget and fluxes in the ocean. However, BPOP can be used to explore the effect of global changes in other physical or biogeochemical processes coupled to the biological pump dynamics. Aside from testing the robustness of our results, the sensitivity tests presented in subsection 5.1.3 serve also as a first exploration of the possibility to apply the model to these further studies. We discuss here a few examples of past changes that could be explored with the present model.

Through Earth's history, variations in the distribution of continents and in the mean sea level height likely impacted the percentage of shelf sea area ( $\mathcal{P}_{\text{shelf}}$ ) throughout the global ocean (Katz et al., 2007). Changes in climate and therefore in the mean temperature are expected to have affected both the air-sea gas exchange of oxygen (Schmidt number,  $N_{\text{Sch}}(T_{\text{mean}})$ ) and vertical mixing ( $\text{Mix}_{\text{vo}}$ ) (Petit et al., 1999). Reduced vertical mixing in warm periods is also expected to be relevant in the future because of global warming (Gruber et al., 2004). Changes in temperature are also known to impact biological activity directly, e.g., by increasing remineralization rates ( $\text{rm}_r$ ) (Laufkötter et al., 2017), and indirectly, e.g., affecting production and mortality rates through changes in the mixed layer depth (Polovina et al., 1995). Lastly, climatic shifts can also cause changes in the intensity of alongshore winds and therefore in the upwelling circulation (~~Upw~~) (Sydemann et al., 2014).

## 6 Conclusions and Outlook

This paper provides a description, evaluation and discussion of the new BPOP model. BPOP is aimed at exploring the effects of changes in the biological pump on the shelf and open ocean nutrient and redox state as well as on P and O fluxes. This model can be adopted for a large variety of studies aimed at exploring the impact of changes in the biological pump, i.e., the particle remineralization length scale  $z_{\text{rem}}$ , in past and future ocean settings. Furthermore, it allows to couple changes in POM properties to changes in the ocean's geometry, circulation and boundary conditions.

Despite its simple representation of the ~~model-ocean~~ circulation and of the biological pump, the model can reasonably simulate values of the current P and O tracer budgets and biological pump fluxes. The model predicts

potentially large variations in these P and O budgets and fluxes for past and future changes in the POM remineralization length. Our preliminary results also indicate that the early ocean may have been nutrient rich, with high levels of production and remineralization and that an anoxic deep shelf setting may have been compatible with an oxygenated deep open ocean.

We plan to apply this model to study the time evolution of the P and O budgets in both the shelf and the open ocean environment across the Neoproterozoic-Phanerozoic transition. Further developments of the model will be aimed at accounting for successive evolutionary innovations, including particle fragmentation due to grazing.

#### **Code availability**

The code is available for download in the supplementary material of the present publication, which also includes the user's manual.

#### **Author contributions**

TL and EL conceived the study. EL conceived and implemented the model. EL and TL evaluated and improved the model. Both authors contributed to the interpretation of the results, and to the writing of the present manuscript.

## Competing interests

The authors declare that they have no conflict of interest.

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<u>Name</u>	<u>Description</u>	<u>Units</u>
<u>P<sup>ss</sup></u>	<u>Inorganic phosphorus in surface shelf sea box</u>	<u>mmol m<sup>-3</sup></u>
<u>P<sup>ds</sup></u>	<u>Inorganic phosphorus in deep shelf sea box</u>	<u>mmol m<sup>-3</sup></u>
<u>P<sup>so</sup></u>	<u>Inorganic phosphorus in surface open ocean box</u>	<u>mmol m<sup>-3</sup></u>
<u>P<sup>do</sup></u>	<u>Inorganic phosphorus in deep open ocean box</u>	<u>mmol m<sup>-3</sup></u>
<u>O<sup>ss</sup></u>	<u>Molecular oxygen in surface shelf box</u>	<u>mmol m<sup>-3</sup></u>

<u><math>O^{ds}</math></u>	<u>Molecular oxygen in deep shelf box</u>	<u>mmol m<sup>-3</sup></u>
<u><math>O^{so}</math></u>	<u>Molecular oxygen in surface open ocean box</u>	<u>mmol m<sup>-3</sup></u>
<u><math>O^{do}</math></u>	<u>Molecular oxygen in deep open ocean box</u>	<u>mmol m<sup>-3</sup></u>
<u><math>O^{at}</math></u>	<u>Oxygen mixing ratio in atmosphere (mol mol<sup>-1</sup>)</u>	<u>-</u>
<u><math>SedP_{org}^s</math></u>	<u>Organic phosphorus in the sediments of the shelf sea</u>	<u>mmol m<sup>-2</sup></u>
<u><math>SedP_{org}^o</math></u>	<u>Organic phosphorus in the sediments of the open ocean</u>	<u>mmol m<sup>-2</sup></u>
<u><math>P^{TOT}</math></u>	<u>Diagnostic variable: total P budget from sources and sinks only</u>	<u>Tmol P</u>
<u><math>O^{TOT}</math></u>	<u>Diagnostic variable: total O budget from sources and sinks only</u>	<u>Pmol O<sub>2</sub></u>

**Table 1: List of the model's state variables and of their units**

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Name	Description	Value	Units	Source
$Mol_{atmo}$	<u>Millimoles of air</u> in atmospheric box	$1.8 \cdot 10^{230}$	<del>mmMoles</del>	-
$\Delta Z_{eu}$	Depth of the euphotic layer in shelf and open ocean	100	m	[1]
$\Delta Z_{ds}$	Depth of the deep shelf sea box	100	m	[2]
$\Delta Z_{do}$	Depth of the deep open ocean box	3500	m	[3]
$A_{ocean}$	Total area covered by the ocean	$361 \cdot 10^{12}$	m <sup>2</sup>	-
$P_{shelf}$	Fraction of the total ocean area currently covered by the shelf sea ( $\leq 200$ m deep)	0.07	-	Barrón and Duarte (2015)

10 **Table 12:** Parameters set that describes the box model's geometry: [1] we assume a constant average euphotic layer depth of 100 m in both shelf and open sea; [2] the shelf sea is assumed to be 200 m deep in total, in line with the definition of shelf sea by Barrón and Duarte (2015); [3] we assume an average open ocean depth of 3600 m (including euphotic layer).

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Name	Description	Value	Units	Source
$P_{ini}$	Initial P concentration for all the ocean boxes	2.2	mmol m <sup>-3</sup>	Watson et al. (2017)
$O_{ini}$	Initial O concentration for all the ocean & atmosphere boxes	0	mmol m <sup>-3</sup>	-
$(P_{org})_{ini}$	Initial $P_{org}$ in all the sediment boxes	0	mmol m <sup>-3</sup>	-

<b>Upw</b>	Upwelling cell mass fluxes	5.5	Sv	Chavez and Messié (2009)
<b>Mix<sub>vo</sub></b>	Vertical mixing in the open ocean	40	Sv	[1]
<b>Mix<sub>ls</sub></b>	Lateral mixing at the surface	1.5	Sv	[2]
<b>Mix<sub>ld</sub></b>	Lateral mixing at depth	1.5	Sv	[2]
<b>Mix<sub>vs</sub></b>	Vertical mixing in the shelf sea	<del>0.51</del>	Sv	[3]
<b>spv</b>	<u>Seconds per year conversion factor (Sv to m<sup>3</sup> yr<sup>-1</sup>)</u>	<u>31557600</u>	<u>s yr<sup>-1</sup></u>	<u>=</u>
<b>P<sub>in</sub></b>	Total P river input	<del>0.092 · 10<sup>12</sup></del>	<del>10<sup>12</sup> · T<sub>in</sub> mmol yr<sup>-1</sup></del>	Slomp and Van Cappellen (2006)
<b>P<sub>open</sub></b>	Fraction of river input delivered to the open ocean	0.4	-	[4]
<b>OP<sub>Red</sub></b>	Oxygen to phosphorus Redfield ratio	106	-	[5]
<b>T<sub>mean</sub></b>	Global mean temperature for oxygen's Schmidt number	17.64	°C	Sarmiento and Gruber (2006)
<b>W<sub>speed</sub></b>	Global mean wind speed for oxygen gas transfer velocity	7.5	m/s	Sarmiento and Gruber (2006)
<b>T<sub>mean</sub></b>	Global mean temperature for oxygen gas transfer velocity	17.64	°C	Sarmiento and Gruber (2006)
<b>K<sub>Henri</sub></b>	Henry's law constant	770 · 10 <sup>-6</sup>	m <sup>3</sup> atm mmol <sup>-1</sup>	-
<b>Omix<sub>0</sub></b>	Today's oxygen mixing ratio in atmosphere	0.21	-	-
<b>W<sub>0</sub></b>	Baseline oxidative weathering flux coefficient	9.752 · 10 <sup>15</sup>	<del>mmol M<sub>mol</sub> yr<sup>-1</sup></del>	[6]

**Table 32:** Parameters set pertaining to the model's initial conditions, circulation mass fluxes, boundary fluxes. Notes: [1] compare to: 38 Sv (Sarmiento and Gruber, 2006), 17 Sv of mixing flux in the Southern Ocean alone (Meyer et al., 2015), estimated open ocean downwelling 38.5 Sv and upwelling 34.5 Sv (Ganachaud and Wunsch, 2000); [2] cross-shelf mass exchange due to lateral recirculation, tides and mixing aimed at including exchange processes other than upwelling (Fennel et al., 2005; Cole et al., 2015; Wollast, 1998); [3] minimal assumption for vertical mixing in nearshore regions due to seasonal and eddy mixing, see also subsection 3.2 Sensitivity to parameter choices; [4] up to 70% of river outflow reaches the open ocean, see Sharples et al. (2017); [5] assuming a constant 1:1=C:O<sub>2</sub> ratio and a Redfield ratio of C:P=106; [6] calculated from the equilibrium solution given P<sub>in</sub>.

Name	Description	Value	Units	Source
<b>P<sub>eff</sub></b>	P maximum uptake <del>rate for production efficiency</del>	0.8	<u>yr<sup>-1</sup></u>	[1]
<b>K<sub>P</sub></b>	Michaelis Menten constant for P uptake	0.2	mmol m <sup>-3</sup>	[2]
<b>K<sub>sO</sub></b>	Michaelis Menten constant for aerobic remineralization <u>in the sediments</u>	<u>0.2</u>	mmol m <sup>-3</sup>	[3]
<b>K<sub>wO</sub></b>	<u>Michaelis Menten constant for aerobic remineralization in the watercolumn</u>	<u>15</u>	<u>mmol m<sup>-3</sup></u>	<u>[4]</u>

<b>cgr</b>	Coagulation rate of small Porg into large Porg	0. <del>36</del> 24	$(\text{mmol m}^{-3})^{-1}$ yr <sup>-1</sup>	[54]
<b>rmr</b>	Remineralization rate of sedimented Porg	0.73	yr <sup>-1</sup>	[54]
<b>fean</b>	Remineralization enhancement factor under anoxia	1.25	=	Slomp and Van Cappellen (2006)
<b>CaPr</b>	Rate of formation of Ca-P mineral from sedimented Porg	<del>0.40</del> 2	$(\text{mmol m}^{-2})^{-1}$ yr <sup>-1</sup>	[65]
<b>fsan</b>	Ca-P formation dampening factor under anoxia	0.5	=	Slomp and Van Cappellen (2006)

Table 43: Parameters set pertaining to the model's Porg cycle and coupled biogeochemical fluxes: [1] maximum P uptake rate, meant to account for environmental limitations of phytoplankton growth rate (such as light and temperature), the magnitude of the rate keeps into account that we are not explicitly resolving phytoplankton concentrations (order of  $10^{-2} \text{ mmolP m}^{-3}$ ), see also production in Gruber et al. (2006) and Yool & Tyrrell (2003); [2] measured values vary in the range of  $0.01 \text{ mmol m}^{-3}$  up to a few  $\text{mmol m}^{-3}$ , varying for different phytoplankton types, see Lomas et al. (2014), Tantanasarit et al. (2013), Krumhardt et al. (2013), Lin et al. (2016), Klausmeier et al. (2004); [3] ~~biogeochemical models commonly switch to anaerobic respiration below  $4 \text{ mmol m}^{-3}$  (Paulmier et al., 2009),~~ measured half-saturation constant for oxygen uptake varies in the range of  $0.1 - 3 \text{ mmol m}^{-3}$  (Ploug, 2001); [4] ~~biogeochemical models commonly switch to anaerobic respiration below  $4 \text{ mmol m}^{-3}$  (Paulmier et al., 2009),~~ measurements suggest a value close to  $19 \text{ mmol m}^{-3}$  (DeVries and Weber, 2017); [5] on the same order of magnitude as Gruber et al. (2006); [5] unmeasured – given the analogous adopted functional form, we assume Ca-P formation to happen on a timescale close to that of P<sub>org</sub> coagulation in the water column.

Quantity	Model	Modern values or estimates	Units	Source
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<u>Total ocean P</u>	<u>3200 - 3400</u>	<u>3100</u>	<u>TmolP</u>	Watson et al. (2017)
<u>Total ocean O<sub>2</sub></u>	<u>100 - 150</u>	<u>220 (deep ocean)</u>	<u>PmolO<sub>2</sub></u>	Slomp and Van Cappellen (2006)
<u>P<sup>ss</sup></u>	<u>1.5 - 1.8</u>	<u>1 - 1.5</u>	<u>mmol m<sup>-3</sup></u>	Garcia et al. (2018b);Sarmiento and Gruber (2006)
<u>P<sup>ds</sup></u>	<u>4.5 - 6</u>	<u>2.2</u>	<u>mmol m<sup>-3</sup></u>	Garcia et al. (2018b);Watson et al. (2017)
<u>P<sup>so</sup></u>	<u>0.5 - 1</u>	<u>0.2 - 2</u>	<u>mmol m<sup>-3</sup></u>	Garcia et al. (2018b);Sarmiento and Gruber (2006)
<u>P<sup>do</sup></u>	<u>2.7 - 3</u>	<u>1 - 3</u>	<u>mmol m<sup>-3</sup></u>	Garcia et al. (2018b);Sarmiento and Gruber (2006)
<u>O<sup>ss</sup></u>	<u>273</u>	<u>200 - 350</u>	<u>mmol m<sup>-3</sup></u>	Garcia et al. (2018a)
<u>O<sup>ds</sup></u>	<u>4 - 20</u>	<u>0-80</u>	<u>mmol m<sup>-3</sup></u>	Garcia et al. (2018a)
<u>O<sup>so</sup></u>	<u>273</u>	<u>200 - 350</u>	<u>mmol m<sup>-3</sup></u>	Garcia et al. (2018a)
<u>O<sup>do</sup></u>	<u>75 - 120</u>	<u>40-200</u>	<u>mmol m<sup>-3</sup></u>	Garcia et al. (2018a)
<u>Production (Prod)</u>	<u>1400 - 3000</u>	<u>3300 - 9000</u>	<u>TmolC yr<sup>-1</sup></u>	Carr et al. (2006)
<u>Export</u>	<u>300 - 430</u>	<u>415 - 1660</u>	<u>TmolC yr<sup>-1</sup></u>	Henson et al. (2011)
<u>Export production</u>	<u>10 % - 32 %</u>	<u>2 % - 20 %</u>	<u>of total Prod</u>	Boyd and Trull (2007)
<u>Burial</u>	<u>0.3 % - 0.7 %</u>	<u>0.4 %</u>	<u>of total Prod</u>	Sarmiento and Gruber (2006)
<u>Shelf sea production</u>	<u>12 % - 20 %</u>	<u>20 %</u>	<u>of total Prod</u>	Barrón and Duarte (2015);Wollast (1998)
<u>Shelf sea export</u>	<u>20 % - 23 %</u>	<u>29 %</u>	<u>of total Export</u>	Sarmiento and Gruber (2006)
<u>Shelf sea burial</u>	<u>100 %</u>	<u>91 %</u>	<u>of total Burial</u>	Sarmiento and Gruber (2006)

**Table 5: Summary of the model evaluation provided in section 3. Modern observations and estimates are compared to model results obtained for  $z_{rem}^L$  in the range of measured values for a modern shelf sea (Cavan et al., 2017).**

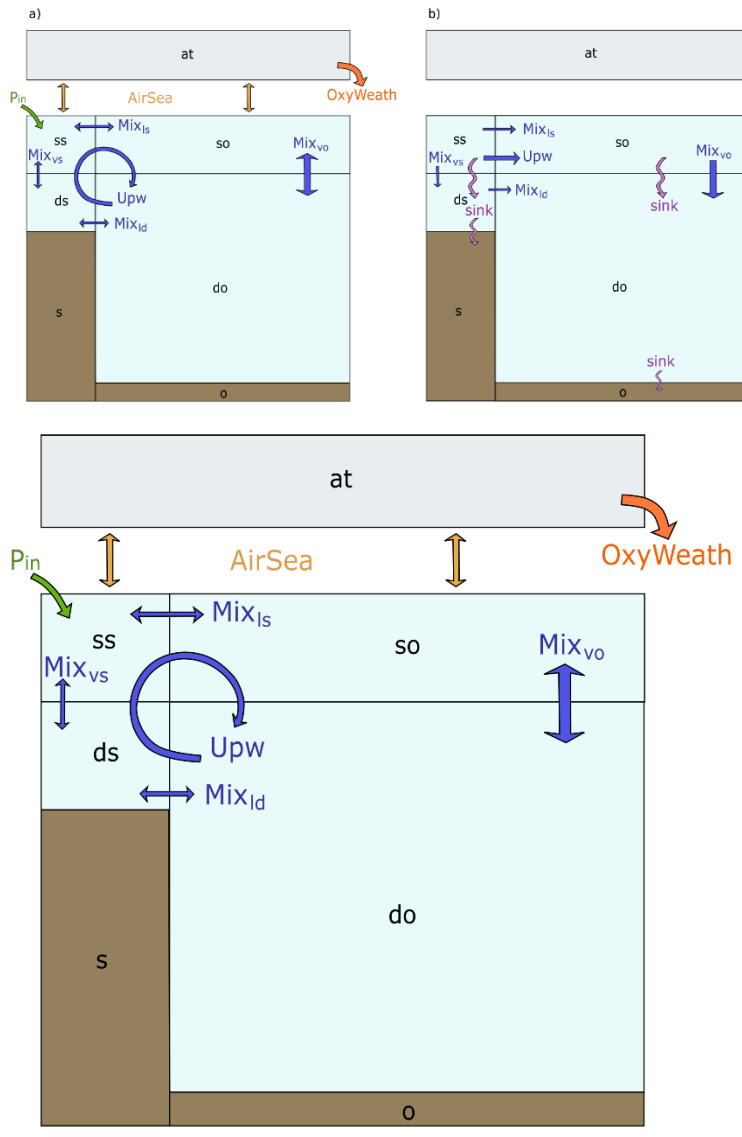


Figure 1: Box model scheme with a representation of **a) the physical and boundary fluxes affecting inorganic tracers the state variables** in the water column and atmosphere, where blue arrows indicate advective and mixing fluxes and yellow arrows indicate air/sea gas exchange fluxes; **b) physical fluxes affecting the implicitly modelled  $P_{org}$  variable, where straight blue arrows indicate advective and mixing fluxes while bent pink arrows indicate gravitational sinking fluxes.** The model includes 7 boxes: surface shelf (ss), deep shelf (ds), surface open ocean (so), deep open ocean (do), atmosphere (at), shelf sediments (s), open ocean sediments (o).

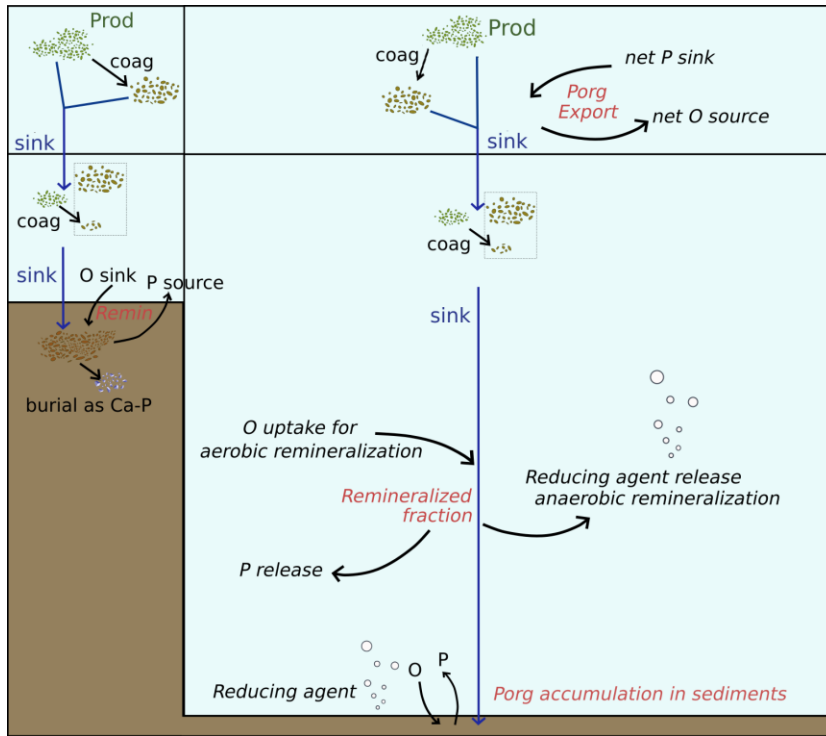
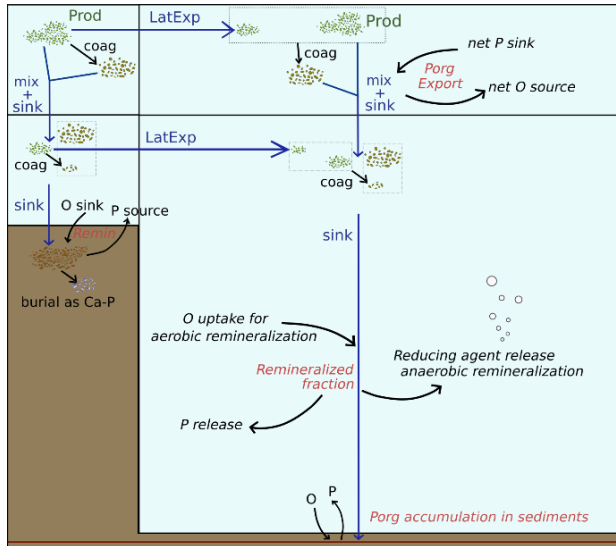
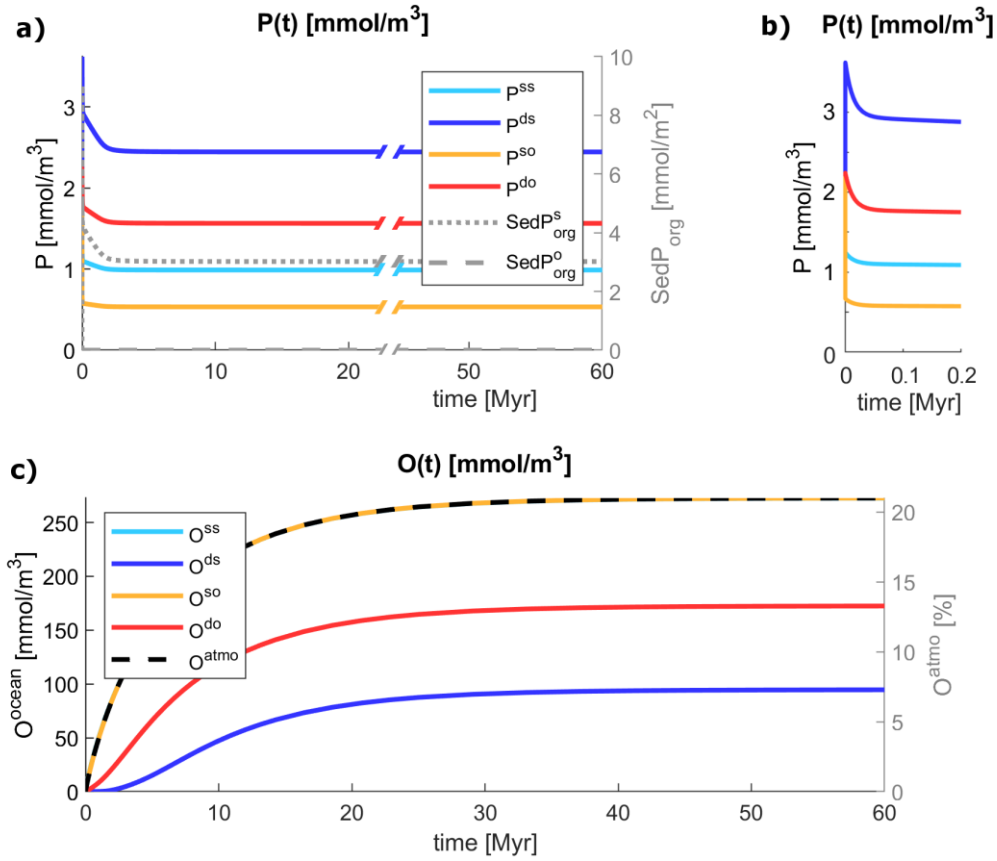
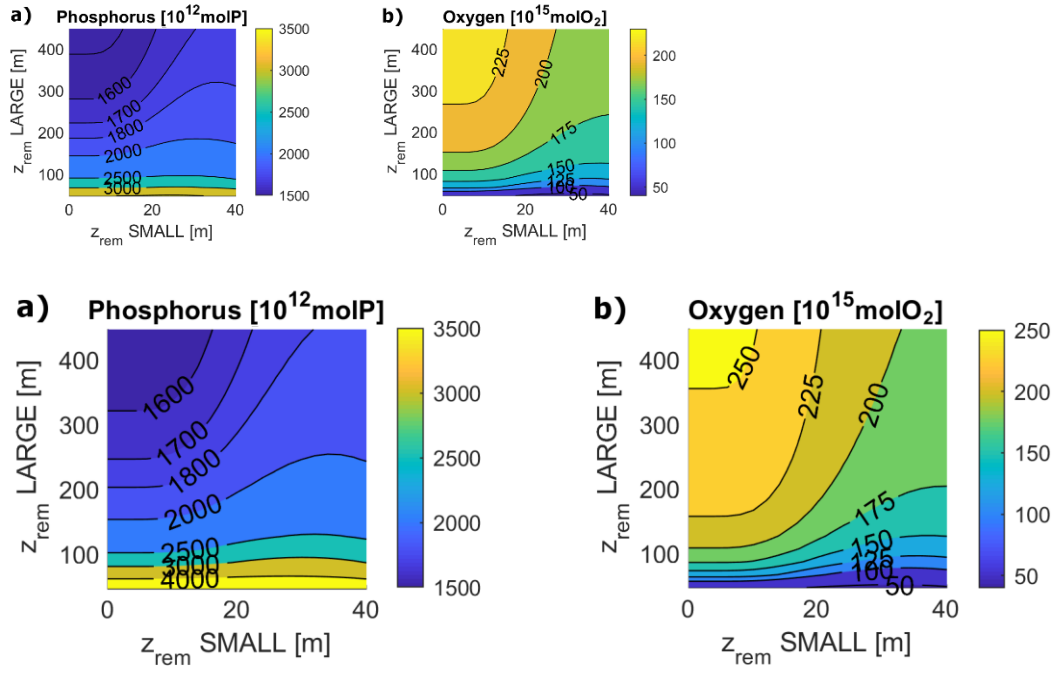


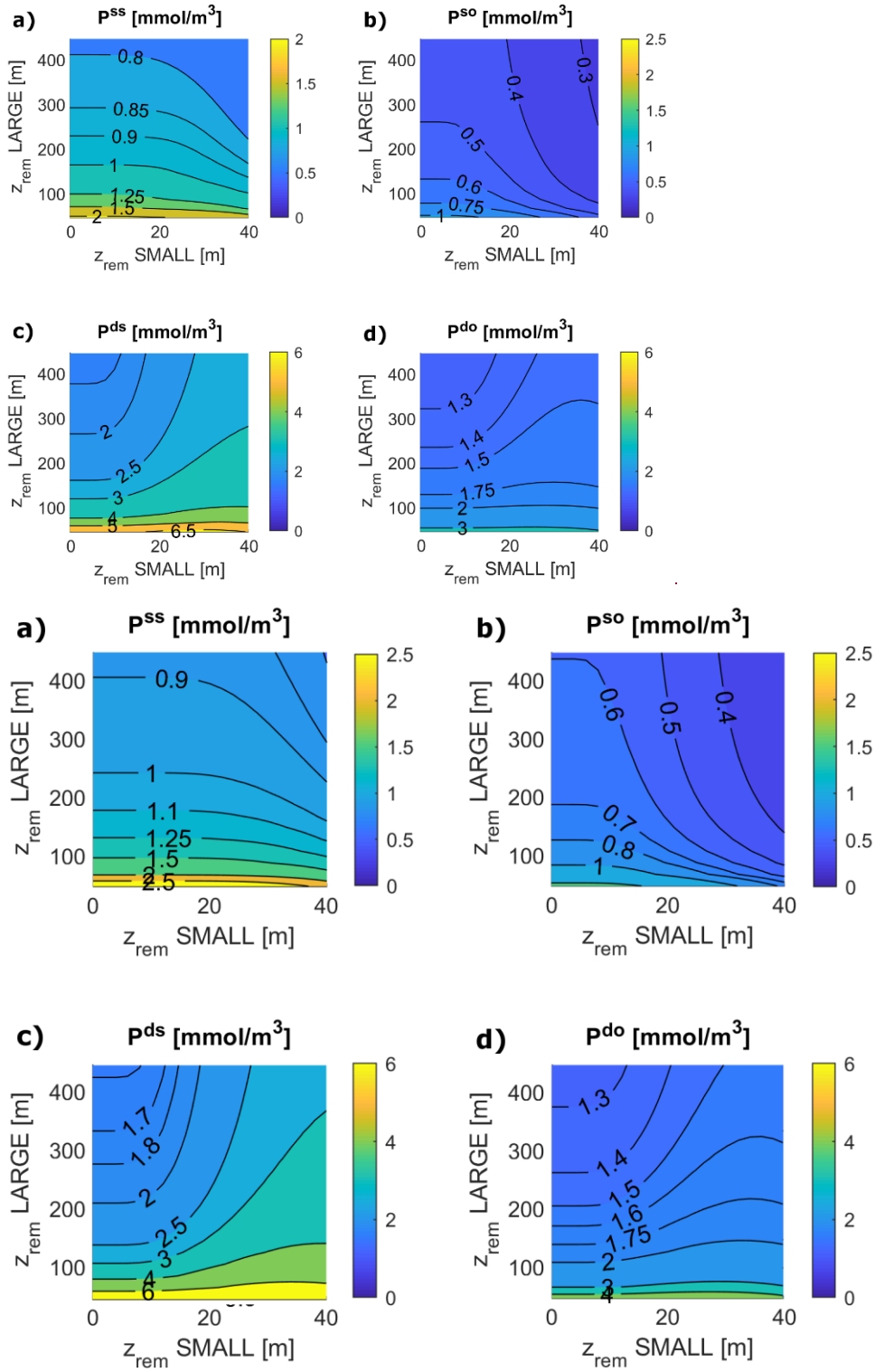
Figure 2: Representation of the physical and biogeochemical fluxes affecting the  $P_{org}$  cycling in the model. Even though some processes (such as burial as Ca-P) are here represented in detail only in one box, the set of biogeochemical processes regulating the  $P_{org}$  dynamics in shelf sea and open ocean (both water column and sediments) is the same, as described in subsection 2.2.



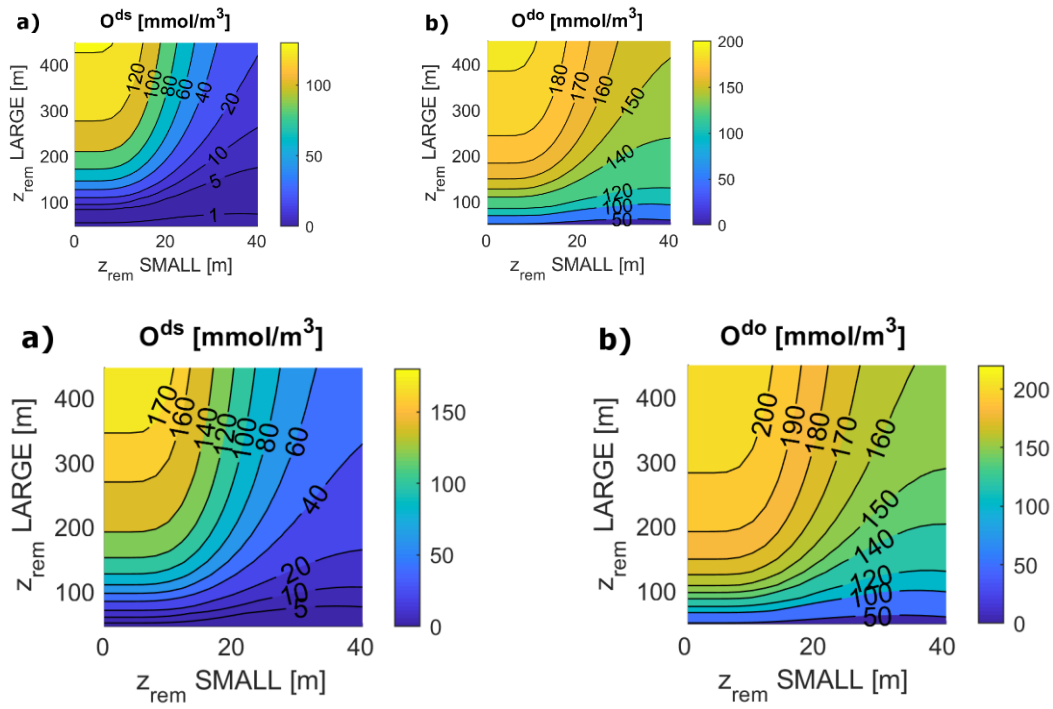
**Figure 3: Evolution of the state variables from the initial conditions listed in Table 2 and remineralization lengths roughly in the middle of the interval of explored values:  $z_{\text{rem}}^{\text{S}} = 20 \text{ m}$ ,  $z_{\text{rem}}^{\text{L}} = 250 \text{ m}$ . (a) Evolution of inorganic phosphorus  $P$  in the water column (left axis) and of organic phosphorus in the sediments  $\text{SedP}_{\text{org}}$  (right axis); (b) zoom on the dynamics of  $P$  in the two hundred thousand years; (c) Evolution of oxygen in the water column (left axis) and atmosphere (right axis). In subplot (c) the two lines  $O^{\text{ss}}$  and  $O^{\text{so}}$  are overlapping: the two variables evolve closely due to the coupling of the surface ocean with the atmosphere via air-sea gas exchange.**



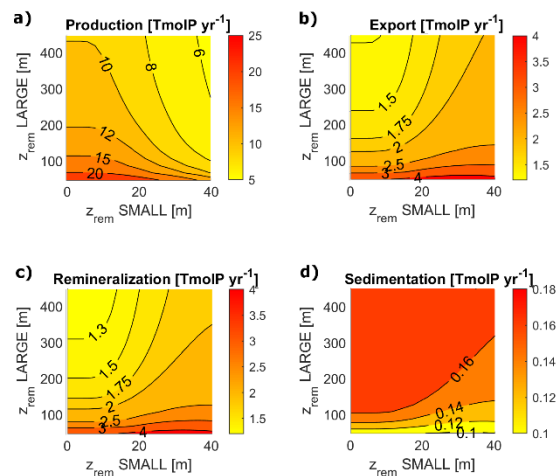
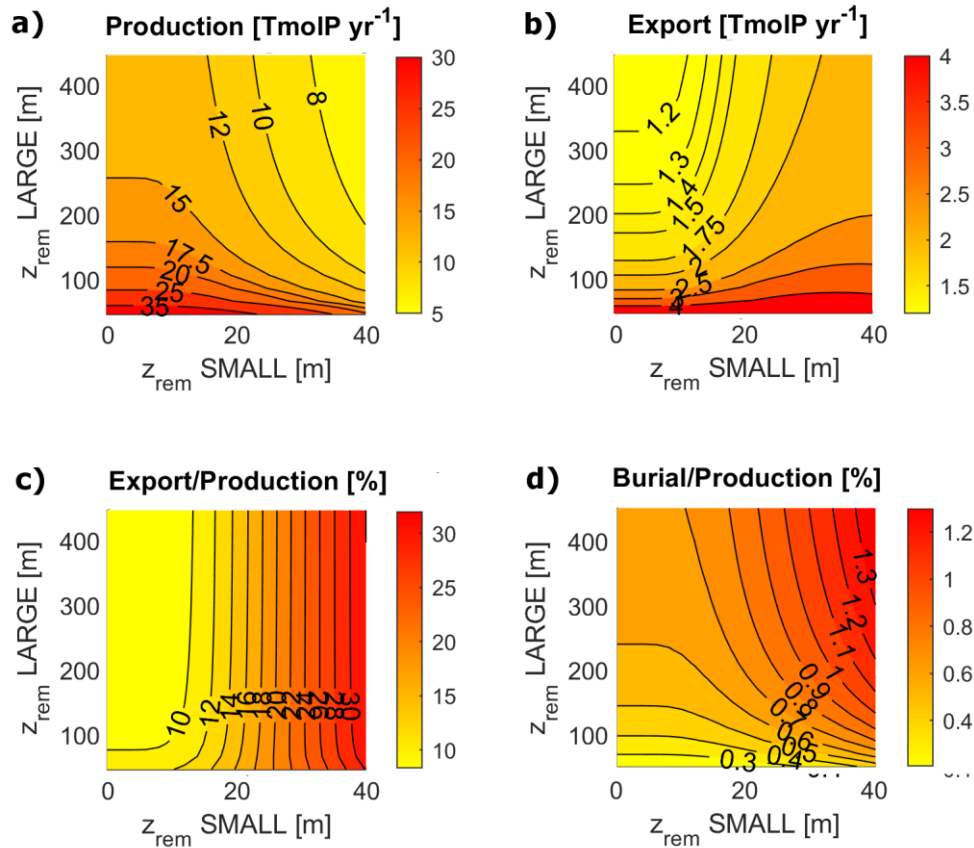
**Figure 43:** Total ocean budgets of (a) P and (b) O at equilibrium for varying  $z_{\text{rem}}^{\text{S}}$  and  $z_{\text{rem}}^{\text{L}}$ .



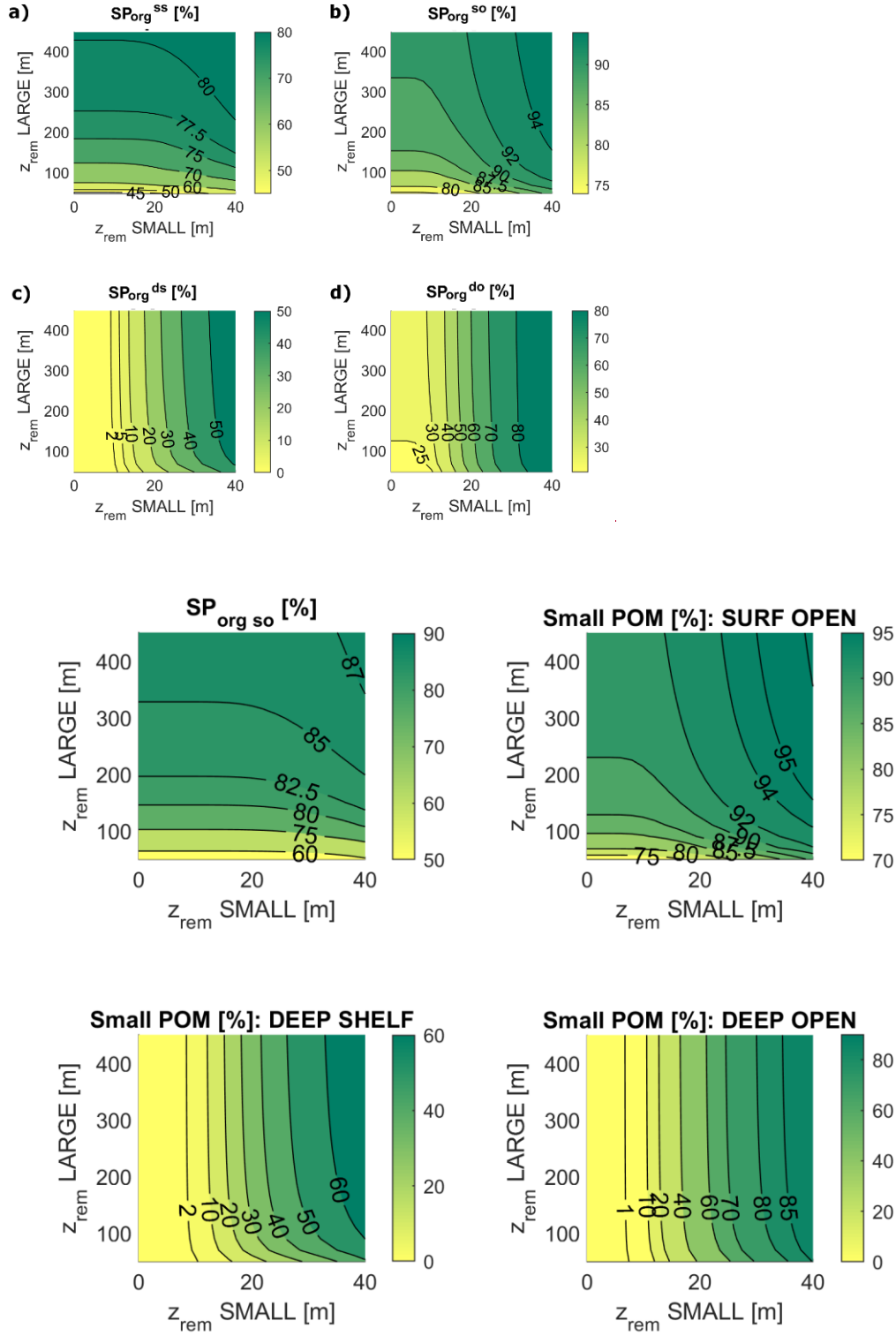
**Figure 54:** Local P concentration in each ocean box for varying  $z_{\text{rem}}^S$  and  $z_{\text{rem}}^L$ : (a) surface shelf sea, ss; (b) surface open ocean, so; (c) deep shelf sea, ds; (d) deep open ocean, do. Surface ocean boxes, as well as deep ocean boxes, are plotted on the same scale.



**Figure 65:** O concentrations at equilibrium for varying  $z_{\text{rem}}^S$  and  $z_{\text{rem}}^L$ : (a) deep shelf sea, ds; (b) deep open ocean, do. Surface ocean boxes (not shown) have nearly constant values of O for any set of  $z_{\text{rem}}$  due to the air-sea gas exchange, which strongly couples them to the atmosphere.



**Figure 76:** Biological pump fluxes in P units for the entire ocean for varying  $z_{\text{rem}}^{\text{S}}$  and  $z_{\text{rem}}^{\text{L}}$ : (a)  $P_{\text{org}}$  surface production; (b)  $P_{\text{org}}$  export through the euphotic layer depth; (c)  ~~$P_{\text{org}}$ -deep-remineralization-in-both-water-column-and~~ Export production, i.e. export to production ratio (d)- ~~Burial to production ratio~~  $P_{\text{org}}$ -sedimentation at the ocean bottom.



**Figure 87:** Small  $P_{org}$  ( $SP_{org}$ ) fraction after coagulation in the surface and at depth for varying  $z_{rem}^S$  and  $z_{rem}^L$ : (a) surface shelf sea, ss; (b) surface open ocean, so; (c) deep shelf sea, ds; (d) deep open ocean, do.

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## Appendix A: Equations

### A.1 Air-sea gas exchange of oxygen

$$N_{Sch} = 1638 - 81.83 \cdot T_{mean} + 1.483 \cdot T_{mean}^2 - 0.008004 \cdot T_{mean}^3 \quad (A1)$$

$$K_W = 0.31 \cdot W_{speed}^2 \cdot \sqrt{660/N_{Sch}} \cdot 10^{-2} \cdot (24 \cdot 365.25); \quad (A2)$$

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### A.2 Surface shelf sea (ss)

$$V^{ss} = \Delta Z_{eu} \cdot A_{ocean} \cdot \mathcal{P}_{shelf} \quad (A3)$$

$$Prod^{ss} = P_{eff} \cdot (P^{ss} / (P^{ss} + K_P)) \cdot P^{ss} \quad (A4)$$

$$SP_{org}^{ss} = Prod^{ss} - cg_r \cdot (Prod^{ss})^2 \quad (A5)$$

$$LP_{org}^{ss} = cg_r \cdot (Prod^{ss})^2 \quad (A6)$$

$$\cancel{LatExp^{ss} = SP_{org}^{ss} \cdot (Upw + Mix_{is}) / V^{ss}} \quad (A7)$$

$$VExp\_SP_{org}^{ss} = \cancel{(SP_{org}^{ss} - LatExp^{ss}) \cdot (\exp(-(\Delta Z_{eu}/2) / z_{rem}^S) + Mix_{ps} / V^{ss})} \quad (A78)$$

$$VExp\_LP_{org}^{ss} = LP_{org}^{ss} \cdot \cancel{(\exp(-(\Delta Z_{eu}/2) / z_{rem}^L) + Mix_{ps} / V^{ss})} \quad (A89)$$

$$\frac{dP^{ss}}{dt} = P_{in} \cdot (1 - \mathcal{P}_{open})/V^{ss} + (Upw \cdot (P^{ds} - P^{ss}) + Mix_{ls} \cdot (P^{so} - P^{ss}) + Mix_{vs} \cdot (P^{ds} - P^{ss})) \cdot spy/V^{ss} - (VExp_{SP_{org}}^{ss} + VExp_{LP_{org}}^{ss})$$

(A10)

5

$$AirSea^{ss} = K_W \cdot (O^{at}/K_{Henri} - O^{ss}) \cdot (A_{ocean} \cdot \mathcal{P}_{shelf})/V^{ss} \quad (A104)$$

$$OProd^{ss} = OP_{Red} \cdot (VExp_{SP_{org}}^{ss} + VExp_{LP_{org}}^{ss}) \quad (A112)$$

$$\frac{dO^{ss}}{dt} = (Upw \cdot (O^{ds} - O^{ss}) + Mix_{ls} \cdot (O^{so} - O^{ss}) + Mix_{vs} \cdot (O^{ds} - O^{ss})) \cdot spy/V^{ss} + AirSea^{ss} + OProd^{ss}$$

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(A123)

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### A.3 Deep shelf sea (ds)

$$V^{ds} = \Delta Z_{ds} \cdot A_{ocean} \cdot \mathcal{P}_{shelf}$$

(A134)

$$VInp_{SP_{org}}^{ds} = VExp_{SP_{org}}^{ss} \cdot (V^{ss}/V^{ds})$$

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(A145)

$$SP_{org}^{ds} = VInp_{SP_{org}}^{ds} - cg_r \cdot (VInp_{SP_{org}}^{ds})^2$$

(A156)

$$LP_{org}^{ds} = VExp_{LP_{org}}^{ss} \cdot (V^{ss}/V^{ds}) + cg_r \cdot (VInp_{SP_{org}}^{ds})^2$$

(A167)

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$$LatExp^{ds} = SP_{org}^{ds} \cdot Mix_{td}/V^{ds} \quad (A18)$$

$$Rem_{SP_{org}}^{ds} = (SP_{org}^{ds} - LatExp^{ds}) \cdot (1 - \exp(-\Delta Z_{ds}/z_{rem}^S))$$

(A179)

$$Rem_{LP_{org}}^{ds} = LP_{org}^{ds} \cdot (1 - \exp(-\Delta Z_{ds}/z_{rem}^L)) \quad (A1820)$$

$$AerRem_{SedP_{org}}^{ds} = rm_r \cdot SedP_{org}^s/\Delta Z_{ds} \cdot (O^{ds}/(O^{ds} + K_0^s K_{\theta}))$$

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(A1924)

$$AnaRem\_SedP_{org}^{ds} = (rm_r \cdot fe_{an}) \cdot SedP_{org}^s / \Delta Z_{ds} \cdot (1 - O^{ds} / (O^{ds} + K_O^s)) \quad (A20)$$

$$\begin{aligned} \frac{dP^{ds}}{dt} = & (Upw \cdot (P^{do} - P^{ds}) + Mix_{ld} \cdot (P^{do} - P^{ds}) + Mix_{vs} \cdot (P^{ss} - P^{ds})) \cdot spy / V^{ds} \\ & ++ (Rem\_SP_{org}^{ds} + Rem\_LP_{org}^{ds} + AerRem\_SedP_{org}^{ds} + AnaRem\_SedP_{org}^{ds}) \\ & + (Rem\_SP_{org}^{ds} + Rem\_LP_{org}^{ds} + Rem\_SedP_{org}^{ds}) \end{aligned}$$

5 (A21)

$$AerRemWcO^{ds} = OP_{Red} \cdot (Rem\_SP_{org}^{ds} + Rem\_LP_{org}^{ds}) \cdot (O^{ds} / (O^{ds} + K_O^w K_O^s))$$

(A22)

$$AerRemSedO^{ds} = OP_{Red} \cdot AerRem\_SedP_{org}^{ds} \quad (A23)$$

$$\begin{aligned} \frac{dO^{ds}}{dt} = & (Upw \cdot (O^{do} - O^{ds}) + Mix_{ld} \cdot (O^{do} - O^{ds}) + Mix_{vs} \cdot (O^{ss} - O^{ds})) \cdot spy / V^{ds} - AerRemWcO^{ds} \\ & - AerRemSedO^{ds} \end{aligned}$$

(A24)

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#### A.4 Surface open ocean (so)

$$V^{so} = \Delta Z_{eu} \cdot A_{ocean} \cdot (1 - \mathcal{P}_{shelf})$$

(A25)

$$Prod^{so} = P_{eff} \cdot (P^{so} / (P^{so} + K_P)) \cdot P^{so}$$

20 (A26)

$$LatInp^{so} = SP_{org}^{ss} \cdot (Upw + Mix_{ls}) / V^{so} \quad (A27)$$

$$SP_{org}^{so} = (Prod^{so} + LatInp^{so}) - cg_r \cdot ((Prod^{so}) + LatInp^{so})^2$$

(A28)

$$LP_{org}^{so} = cg_r \cdot (Prod^{so} + LatInp^{so})^2$$

25 (A29)

$$VExp\_SP_{org}^{so} = SP_{org}^{so} \cdot (\exp(-(\Delta Z_{eu}/2) / z_{rem}^S) + Mix_{vo} / V^{so})$$

(A30)

$$VExp\_LP_{org}^{so} = LP_{org}^{so} \cdot (\exp(-(\Delta Z_{eu}/2) / z_{rem}^L) + Mix_{vo} / V^{so})$$

(A31)

$$\frac{dP^{so}}{dt} = P_{in} \cdot \mathcal{P}_{open}/V^{ss} + (Upw \cdot (P^{ss} - P^{so}) + Mix_{ls} \cdot (P^{ss} - P^{so}) + Mix_{vo} \cdot (P^{do} - P^{so})) \cdot spy/V^{so} \\ - (VExp\_SP_{org}^{so} + VExp\_LP_{org}^{so}) +$$

$$\frac{(VExp\_SP_{org}^{so} + VExp\_LP_{org}^{so})}{V^{so}}$$

(A313)

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$$AirSea^{so} = K_W \cdot (O^{at}/K_{Henri} - O^{so}) \cdot (A_{ocean} \cdot (1 - \mathcal{P}_{shelf}))/V^{so}$$

(A324)

$$OProd^{so} = OP_{Red} \cdot (VExp\_SP_{org}^{so} + VExp\_LP_{org}^{so})$$

(A335)

$$10 \quad \frac{dO^{so}}{dt} = (Upw \cdot (O^{ss} - O^{so}) + Mix_{ls} \cdot (O^{ss} - O^{so}) + Mix_{vo} \cdot (O^{do} - O^{so})) \cdot spy/V^{so} + AirSea^{so} \\ + OProd^{so}$$

(A346)

## A.5 Deep open ocean (do)

$$15 \quad V^{do} = \Delta Z_{do} \cdot A_{ocean} \cdot (1 - \mathcal{P}_{shelf})$$

(A357)

$$VInp\_SP_{org}^{do} = VExp\_SP_{org}^{so} \cdot (V^{so}/V^{do})$$

(A368)

$$LatInp^{do} = SP_{org}^{do} \cdot Mix_{la}/V^{do} \quad (A39)$$

$$20 \quad SP_{org}^{do} = (VInp\_SP_{org}^{do} + LatInp^{do}) - cg_r \cdot (VInp\_SP_{org}^{do} + LatInp^{do})^2$$

(A3740)

$$LP_{org}^{do} = VExp\_LP_{org}^{so} \cdot (V^{so}/V^{do}) + cg_r \cdot (VInp_{SP_{org}}^{do} + LatInp^{do})^2$$

(A3841)

$$Rem\_SP_{org}^{do} = SP_{org}^{do} \cdot (1 - \exp(-\Delta Z_{do}/z_{rem}^S)) \quad (A3942)$$

$$25 \quad Rem\_LP_{org}^{do} = LP_{org}^{do} \cdot (1 - \exp(-\Delta Z_{do}/z_{rem}^L)) \quad (A403)$$

$$AerRem\_SedP_{org}^{do} = rm_r \cdot SedP_{org}^o/\Delta Z_{do} \cdot (O^{do}/(O^{do} + K_O^S K_{\theta}))$$

(A414)

$$AnaRem\_SedP_{org}^{do} = (rm_r \cdot fe_{an}) \cdot SedP_{org}^o/\Delta Z_{do} \cdot (1 - O^{do}/(O^{do} + K_O^S)) \quad (A42)$$

$$\begin{aligned} \frac{dP^{do}}{dt} = & (Upw \cdot (P^{so} - P^{do}) + Mix_{ld} \cdot (P^{ds} - P^{do}) + Mix_{vo} \cdot (P^{so} - P^{do})) \cdot spy / V^{do} \\ & + (Rem\_SP_{org}^{do} + Rem\_LP_{org}^{do} + AerRem\_SedP_{org}^{do} + AnaRem\_SedP_{org}^{do}) + \\ & + (\cancel{Rem\_SP_{org}^{do}} + \cancel{Rem\_LP_{org}^{do}} + \cancel{Rem\_SedP_{org}^{do}}) \end{aligned} \quad (A435)$$

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$$AerRemWcO^{do} = OP_{Red} \cdot (Rem\_SP_{org}^{do} + Rem\_LP_{org}^{do}) \cdot (O^{do} / (O^{do} + K_O^w K_a)) \quad (A446)$$

$$AerRemSedO^{do} = OP_{Red} \cdot AerRem\_SedP_{org}^{do} \quad (A457)$$

$$\begin{aligned} \frac{dO^{do}}{dt} = & (Upw \cdot (O^{so} - O^{do}) + Mix_{ld} \cdot (O^{ds} - O^{do}) + Mix_{vo} \cdot (O^{so} - O^{do})) \cdot spy / V^{do} - AerRemWcO^{do} \\ & - AerRemSedO^{do} \end{aligned} \quad (A4648)$$

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#### A.6 Shelf sea sediments (s)

$$\begin{aligned} SedFlx^s = & (\cancel{SP_{org}^{ds}} - \cancel{LatExp^{ds}}) \cdot \exp(-\Delta Z_{ds} / z_{rem}^s) + LP_{org}^{ds} \cdot \exp(-\Delta Z_{ds} / z_{rem}^L) \cdot \Delta Z_{ds} \\ & CaPform^s = CaP_r \cdot (SedP_{org}^s)^2 \cdot (O^{ds} / (O^{ds} + K_O^w) + f_{san} \cdot (1 - O^{ds} / (O^{ds} + K_O^w))) \end{aligned} \quad (A4749)$$

$$Rem\_SedP_{org}^{ds} = AerRem\_SedP_{org}^{ds} + AnaRem\_SedP_{org}^{ds} \quad (A49)$$

$$\frac{dSedP_{org}^s}{dt} = SedimFlx^s - CaPform^s - Rem\_SedP_{org}^{ds} \cdot \Delta Z_{ds} \quad (A5054)$$

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#### 25 A.7 Open ocean sediments (o)

$$\begin{aligned} SedFlx^o = & (\cancel{SP_{org}^{do}} - \cancel{LatExp^{do}}) \cdot \exp(-\Delta Z_{dos} / z_{rem}^s) + LP_{org}^{do} \cdot \exp(-\Delta Z_{dos} / z_{rem}^L) \cdot \Delta Z_{do} \\ & CaPform^o = CaP_r \cdot (SedP_{org}^o)^2 \cdot (O^{do} / (O^{do} + K_O^w) + f_{san} \cdot (1 - O^{do} / (O^{do} + K_O^w))) \end{aligned} \quad (A512)$$

$$Rem\_SedP_{org}^{do} = AerRem\_SedP_{org}^{do} + AnaRem\_SedP_{org}^{do} \quad (A53)$$

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$$\frac{dSedP_{org}^o}{dt} = Sed_{im}Flx^o - CaPform^o - Rem_{SedP_{org}}^{do} \cdot \Delta Z_{do}$$

(A544)

## 5 A.8 Atmosphere (at)

$$AirSea^{at} = (AirSea^{ss} + AirSea^{so}) / (Mol_{atmo} \cdot 10^3) \quad (A555)$$

$$AnaRemWc^{ds} = OP_{Red} \cdot (Rem_{SP_{org}}^{ds} + Rem_{LP_{org}}^{ds}) \cdot (1 - O^{ds} / (O^{ds} + K_O^w K_{eq}))$$

(A5656)

$$AnaRemWc^{do} = OP_{Red} \cdot (Rem_{SP_{org}}^{do} + Rem_{LP_{org}}^{do}) \cdot (1 - O^{do} / (O^{do} + K_O^w K_{eq}))$$

(A5757)

$$AnaRemWc^{at} = (AnaRemWc^{ds} \cdot V^{ds} + AnaRemWc^{do} \cdot V^{do}) / (Mol_{atmo} \cdot 10^3)$$

(A5858)

$$AnaRemSed^{at} = (AnaRem_{SedP_{org}}^{ds} \cdot V^{ds} + AnaRem_{SedP_{org}}^{do} \cdot V^{do}) / Mol_{atmo} \quad (A59)$$

$$OxyWeath = W_0 \cdot \sqrt{O^{at} / Omix_0} / (Mol_{atmo} \cdot 10^3) \quad (A6059)$$

$$\frac{dO^{at}}{dt} = -AirSea^{at} - AnaRemWc^{at} - OxyWeath$$

(A610)

## A.9 Diagnostics: Total budgets of P and O

$$P_{sources} = P_{in} \cdot 10^{-15} \quad (A62)$$

$$P_{sinks} = (CaPform^s \cdot A_{ocean} \cdot \mathcal{P}_{shelf} + CaPform^o \cdot A_{ocean} \cdot (1 - \mathcal{P}_{shelf})) \cdot 10^{-15} \quad (A63)$$

$$\frac{dP^{TOT}}{dt} = P_{sources} - P_{sinks}$$

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(A64)

$$O_{sources} = (OProd^{ss} \cdot V^{ss} + OProd^{so} \cdot V^{so}) \cdot 10^{-18} \quad (A65)$$

5  $O_{sinks} = ((SedRemO^{ds} + AerRem^{ds}) \cdot V^{ds} + (SedRemO^{do} + AerRem^{do}) \cdot V^{do} + OxyWeath \cdot (Mol_{atmo} \cdot 10^3)) \cdot 10^{-18} \quad (A66)$

$$\frac{dO^{tot}}{dt} = O_{sources} - O_{sinks}$$

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(A67)

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