https://doi.org/10.5194/gmd-2019-182
Preprint. Discussion started: 14 August 2019
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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_{rem}) scheme. We independently vary z_{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 lay close to present estimates for z_{rem} in the range of currently measured values. Our results highlight that relatively small changes in z_{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 that shelf ocean anoxia can coexist with an oxygenated deep open ocean for realistic values of z_{rem}, especially for large values of the small particle z_{rem}. This could challenge conventional interpretations that the Proterozoic deep ocean was anoxic, which 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 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 (O_2 < 60 mmol m^{-3}), suboxic (O_2 < 5 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

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Geoscientific Model Development Discussions

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

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Geoscientific Model Development Discussions

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 model resolves explicitly three types of tracers: molecular oxygen O_2 (O), inorganic dissolved phosphorus (P) and sedimented organic phosphorus ($SedP_{org}$). 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 1, while the set of parameters adopted for the modelled physical and geochemical fluxes can be found in Table 2.

2.1.1 Box properties and physical fluxes

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 a 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

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

For each surface box *i*, air-sea gas exchange allows O fluxes between the 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:

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

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

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Geoscientific Model Development Discussions

ocean (Sharples et al., 2017). At equilibrium, the P_{org} burial flux must balance P_{in}. Oxidative weathering determined by atmospheric (at) O 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 $Omix_0$ (Lenton et al., 2018), following:

$$\boldsymbol{OxyWeath = W_0 \cdot \sqrt{O^{at}/Omix_0}} \quad (3)$$

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 3.

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 Porg 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:

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

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:

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

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

The implicit representation of the organic matter in the water column implies that no organic matter is accumulated in the ocean, 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 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

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Preprint. Discussion started: 14 August 2019
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Geoscientific Model Development Discussions

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). 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:

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

where $\boldsymbol{f_0^k}$ is the flux at the reference depth $\boldsymbol{z_0}$, and the index $\boldsymbol{k}$ 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 $\boldsymbol{z_0}$ (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

SPorg and LPorg accumulate in the sediments as $SedP_{org}$, which is calculated as a density per unit 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:

$$\boldsymbol{SedFlx^i = \left(SP_{org}{}^j \cdot exp\left(-\Delta Z_j / z_{rem}^S\right) + LP_{org}{}^j \cdot exp\left(-\Delta Z_j / z_{rem}^L\right)\right) \cdot \Delta Z_j} \quad (7)$$

The accumulated $SedP_{org}$ 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 $SedP_{org}$ 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_r:

$$\boldsymbol{CaPform^i = CaP_r \cdot \left(SedP_{org}{}^i\right)^2} \quad (8)$$

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

https://doi.org/10.5194/gmd-2019-182
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Geoscientific Model Development Discussions

2.2.5 Remineralization in the water column and sediments

At each time step, remineralization in the water column completely depletes the P_{org} that has not reached the sediments. In the two surface boxes, remineralization of P_{org} 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_{org} 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:

$$\boldsymbol{VExp^i = {SP_{org}}^i \cdot exp(-(\Delta Z_{eu}/2)\,/z^S_{rem}) + {LP_{org}}^i \cdot exp(-(\Delta Z_{eu}/2)\,/z^L_{rem}) + ({SP_{org}}^i + {LP_{org}}^i) \cdot Mix_{ij}/V^i} \quad (9)$$

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

$$\boldsymbol{WcRem^j = {SP_{org}}^j \cdot (1 - exp(-\Delta Z_j\,/z^S_{rem})) + {LP_{org}}^i \cdot (1 - exp(-\Delta Z_j\,/z^L_{rem}))} \quad (10)$$

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_O. Anaerobic remineralization takes up the entire remaining P_{org} that is not remineralized aerobically and releases a product which "bubbles up" to the atmosphere, reacting with atmospheric oxygen.

In each sediment box *i*, aerobic remineralization of $SedP_{org}$ takes up oxygen from the overlaying deep-water box *j* and happens at a constant rate which is limited by a Michaelis-Menten coefficient, analogously to aerobic remineralization in the deep water-column. This flux is regulated by a constant remineralization rate coefficient rm_r as in:

$$\boldsymbol{SedRem^i = rm_r \cdot {SedP_{org}}^i \cdot (O^j/(O^j + K_O))} \quad (11)$$

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 $SedP_{org}$ in the surface ocean (s), deep ocean (d), atmosphere (at) and sediments, without distinguishing between coastal and open ocean boxes. 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.

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

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

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

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

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

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

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Geoscientific Model Development Discussions

Where: P_{in} 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_{org} 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 $SedP_{org}$ in P units (only aerobic); AirseaFlx represents the air-sea flux exchange of O; OxyWeath is the O weathering flux sink; SedFlx is the $SedP_{org}$ 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 zrem 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

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 account 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 (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.

In this range, 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 2500 TmolP and 150 $PmolO_2$ in the entire ocean, compared to the estimated total P reservoir of 3100 TmolP (Watson et al., 2017) and estimated deep ocean O_2 reservoir of 220 $PmolO_2$ (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 [3.5 mmol m^{-3}, 4.5 mmol m^{-3}] and [3 mmol m^{-3}, 5 mmol m^{-3}] respectively (Figure 4,5). In the deep open ocean, P and O concentrations shift to about 2.2 mmol m^{-3} and 120 mmol m^{-3} respectively, with minor changes for varying z_{rem}^S. For any combination of z_{rem}^S and z_{rem}^L, O levels in surface ocean boxes lay around 272.5 mmol m^{-3}, a good approximation of average modern surface values (Garcia et al., 2018). In general, the deep shelf always shows the highest P values and lowest O concentrations

https://doi.org/10.5194/gmd-2019-182
Preprint. Discussion started: 14 August 2019
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Geoscientific Model Development Discussions

compared to the other ocean regions, while, as expected, the surface shelf sea is richer in P compared to the surface open ocean.

Biological fluxes, such as production, export and burial, are lower but of the same order of magnitude of present estimates (Figure 6). 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 an equivalent C primary production of between 1000 TmolC yr^{-1} and 1800 TmolC yr^{-1}, calculated using a fixed C:P Redfield ratio of 106. This must be compared to an expected value of at least 3300 TmolC yr^{-1}, reaching up to more than 9000 TmolC yr^{-1} according to satellite estimates (Carr et al., 2006). Export below the euphotic layer ranges between 250 TmolC yr^{-1} and 300 TmolC yr^{-1}, compared to an estimated value that lays between 415 TmolC yr^{-1} and 1660 TmolC yr^{-1} (Henson et al., 2011). Even though the absolute values of the fluxes are lower than expected, the relative magnitude of the fluxes compared to production lay in the range of present estimates. The modelled export corresponds to between 15 % and 35 % of total production, strongly depending on z_{rem}^{S}, compared to an expected range of 2 % - 20 % (Boyd and Trull, 2007). Buried P_{org} corresponds to between 0.4 % and 0.8 % 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% 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 % 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_{rem} compared to observations (Cavan et al., 2017;Lam et al., 2011) due to our choice of using the same value of z_{rem}^{S} and z_{rem}^{L} for both the coastal and the open ocean box. This simplifying assumption limits the capacity of P_{org} 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 3). 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 4,5), which are coupled to high levels of production and remineralization and low rates of sedimentation (Figure 6). 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 272 mmol m^{-3}) and, for most values, also to maintain the deep ocean above the level of hypoxia (Figure 5). 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^{-3}) for 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

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Preprint. Discussion started: 14 August 2019
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Geoscientific Model Development Discussions

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_{org} properties due to the rather irrelevant contribution of SP_{org} 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 20 % for low z_{rem}^{S} and 40 % for high z_{rem}^{S}, an overall trend that affects also the ratio of deep remineralization to surface production (Figure 6).

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^{-3} and 6.5 mmol m^{-3}, while O levels lay between 1 mmol m^{-3} and 200 mmol m^{-3}. Production in carbon units lays in the interval [600 TmolC yr^{-1}, 2200 TmolC yr^{-1}].

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_{org} into LP_{org} after production in surface boxes affects between 20 % and 50 % of the small particles in the shelf sea and between 5 % and 25 % of the small particles in the open ocean (Figure 7a,b). The highest rates of coagulation of SP_{org} into LP_{org} 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 (≤ 6 % of the exported SP_{org}). Small particles contribute between 5 % and 50 % to export and between 5 % and 15 % 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 between 30 % and 80 % 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.

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Geoscientific Model Development Discussions

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

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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}, 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 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 budget, but they do impact O. For lower Mix_{vo}, the O budget decreases due to lower O storage at depth. Changes in vertical mixing on the shelf (Mix_{vs}), instead, have a minor impact on the model's budgets and fluxes. 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.

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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_{rem}^{L} measured for modern shelf environment (Cavan et al., 2017) modelled equilibrium budgets and fluxes are very sensitive to small changes in z_{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 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_{rem}^{S} and z_{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

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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 ($\mathcal{P}_{shelf}$) throughout the global ocean (Katz et al., 2007). Changes climate and therefore in the mean temperature are expected to have affected both the air-sea gas exchange of oxygen (Schmidt number, $N_{Sch}(T_{mean})$) and vertical mixing (Mix_{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 (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) (Sydeman 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_{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 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.

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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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Name	Description	Value	Units	Source
$\mathbf{Mol_{atmo}}$	Moles in atmospheric box	$1.8 \cdot 10^{20}$	Moles	-
$\mathbf{\Delta Z_{eu}}$	Depth of the euphotic layer in shelf and open ocean	100	m	[1]
$\mathbf{\Delta Z_{ds}}$	Depth of the deep shelf sea box	100	m	[2]
$\mathbf{\Delta Z_{do}}$	Depth of the deep open ocean box	3500	m	[3]
$\mathbf{A_{ocean}}$	Total area covered by the ocean	$361 \cdot 10^{12}$	m^2	-
$\mathbf{\mathcal{P}_{shelf}}$	Fraction of the total ocean area currently covered by the shelf sea (≤ 200 m deep)	0.07	-	Barrón and Duarte (2015)

Table 1: 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).

Name	Description	Value	Units	Source
$\mathbf{P_{ini}}$	Initial P concentration for all the ocean boxes	2.2	mmol m^{-3}	Watson et al. (2017)
$\mathbf{O_{ini}}$	Initial O concentration for all the ocean & atmosphere boxes	0	mmol m^{-3}	-
$\mathbf{(P_{org})_{ini}}$	Initial P_{org} in all the sediment boxes	0	mmol m^{-3}	-
Upw	Upwelling cell mass fluxes	5.5	Sv	Chavez and Messié (2009)
$\mathbf{Mix_{vo}}$	Vertical mixing in the open ocean	40	Sv	[1]
$\mathbf{Mix_{ls}}$	Lateral mixing at the surface	1.5	Sv	[2]
$\mathbf{Mix_{ld}}$	Lateral mixing at depth	1.5	Sv	[2]
$\mathbf{Mix_{vs}}$	Vertical mixing in the shelf sea	0.5	Sv	[3]
$\mathbf{P_{in}}$	Total P river input	0.092	Tmol yr^{-1}	Slomp and Van Cappellen (2006)
$\mathbf{\mathcal{P}_{open}}$	Fraction of river input delivered to the open ocean	0.4	-	[4]
$\mathbf{OP_{Red}}$	Oxygen to phosphorus Redfield ratio	106	-	[5]
$\mathbf{T_{mean}}$	Global mean temperature for oxygen's Schmidt number	17.64	°C	Sarmiento and Gruber (2006)

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W_{speed}	Global mean wind speed for oxygen gas transfer velocity	7.5	m/s	Sarmiento and Gruber (2006)
T_{mean}	Global mean temperature for oxygen gas transfer velocity	17.64	ºC	Sarmiento and Gruber (2006)
K_{Henri}	Henry's law constant	$770 \cdot 10^{-6}$	m^3 atm $mmol^{-1}$	-
$Omix_0$	Today's oxygen mixing ratio in atmosphere	0.21	-	-
W_0	Baseline oxidative weathering flux coefficient	$9.752 \cdot 10^{15}$	mmol	[6]

Table 2: 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_2 ratio and a Redfield ratio of C:P=106; [6] calculated from the equilibrium solution given P_{in}.

Name	Description	Value	Units	Source
P_{eff}	P maximum uptake efficiency	0.8	-	[1]
K_P	Michaelis Menten constant for P uptake	0.2	mmol m^{-3}	[2]
K_O	Michaelis Menten constant for aerobic remineralization	2	mmol m^{-3}	[3]
cg_r	Coagulation rate of small Porg into large Porg	0. 36	yr^{-1}	[4]
rm_r	Remineralization rate of sedimented Porg	0.73	yr^{-1}	[4]
CaP_r	Rate of formation of CaP mineral from sedimented Porg	0.2	yr^{-1}	[5]

Table 3: Parameters set pertaining to the model's Porg cycle and coupled biogeochemical fluxes: [1] maximum P uptake meant to account for environmental limitations of phytoplankton growth rate; [2] measured values vary in the range of 0.01 mmol m^{-3} up to a few 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 mmol m^{-3} (Paulmier et al., 2009), measured half-saturation constant for oxygen uptake varies in the range of 0.1 - 3 mmol m^{-3} (Ploug, 2001); [4] 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_{org} coagulation in the water column.

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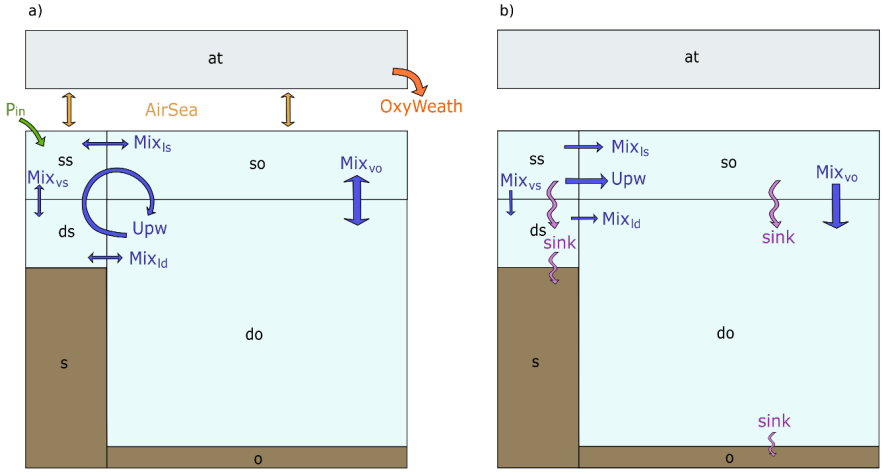


Figure 1: Box model scheme with a representation of: a) physical and boundary fluxes affecting the state variables in the water column and atmosphere, where blue arrows indicate advective and mixing fluxes and yellow arrows indicate air/sea gas exchange fluxes; b) physical fluxes affecting the implicitly modelled Porg 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).

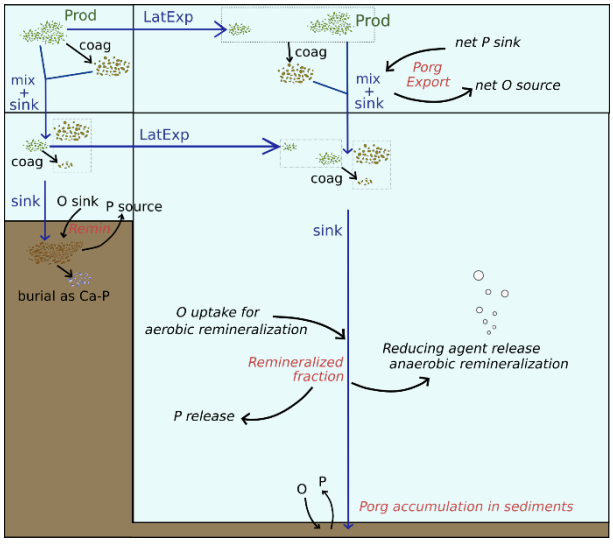
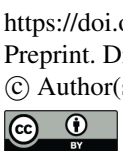


Figure 2: Representation of the physical and biogeochemical fluxes affecting the P_{org} cycling in the model. Even though some processes (such as burial as Ca-P) are here represented in detail only in one box, the set of biogeochemical processes regulating the P_{org} dynamics in shelf sea and open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

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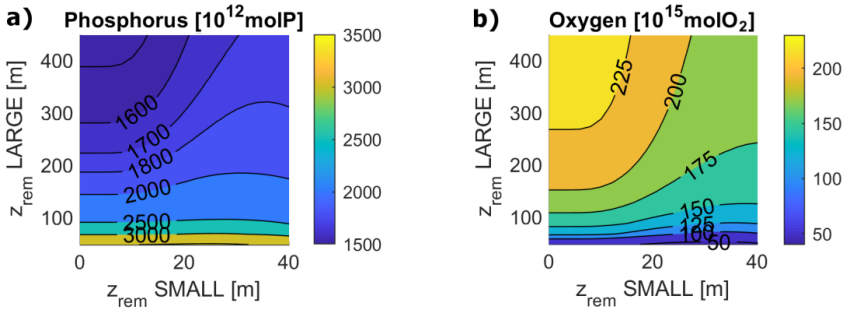


Figure 3: Total ocean budgets of (a) P and (b) O at equilibrium for varying z_{rem}^S and z_{rem}^L.

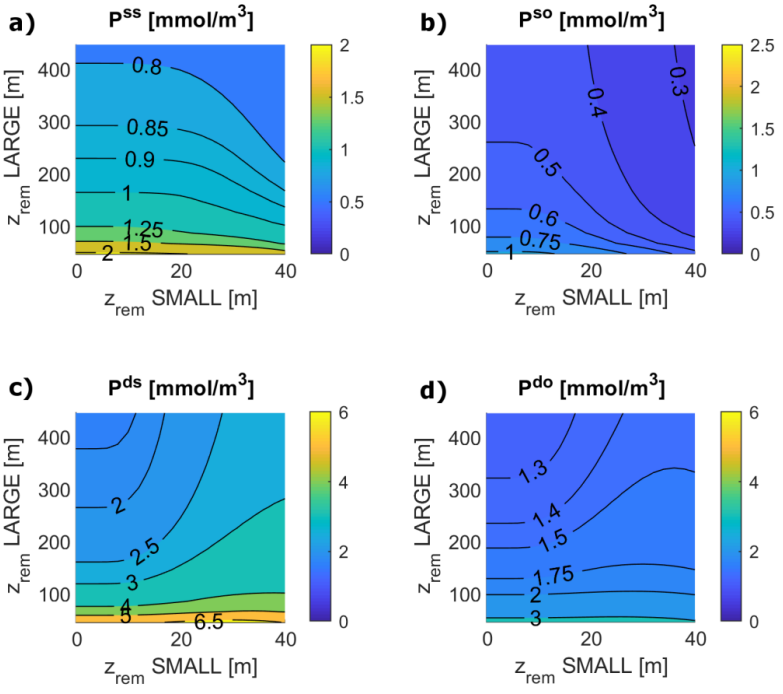
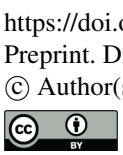


Figure 4: Local P concentration in each ocean box for varying z_{rem}^S and z_{rem}^L: (a) surface shelf sea, ss; (b) surface open ocean, so; (c) deep shelf sea, ds; (d) deep open ocean, do. Surface ocean boxes, as well as deep ocean boxes, are plotted on the same scale.

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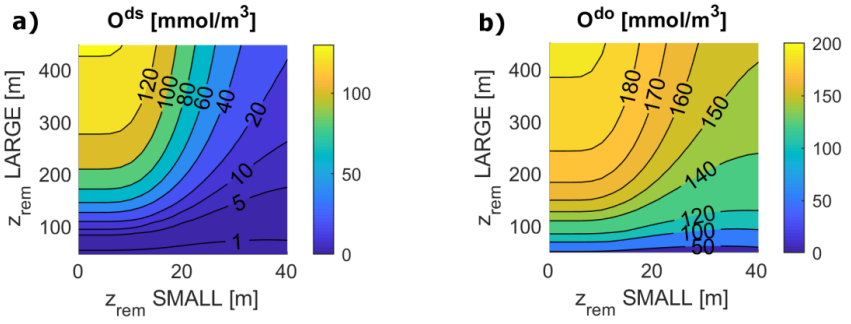


Figure 5: O concentrations at equilibrium for varying z_{rem}^S and z_{rem}^L: (a) deep shelf sea, ds; (b) deep open ocean, do. Surface ocean boxes (not shown) have nearly constant values of O for any set of z_{rem} due to the air-sea gas exchange, which strongly couples them to the atmosphere.

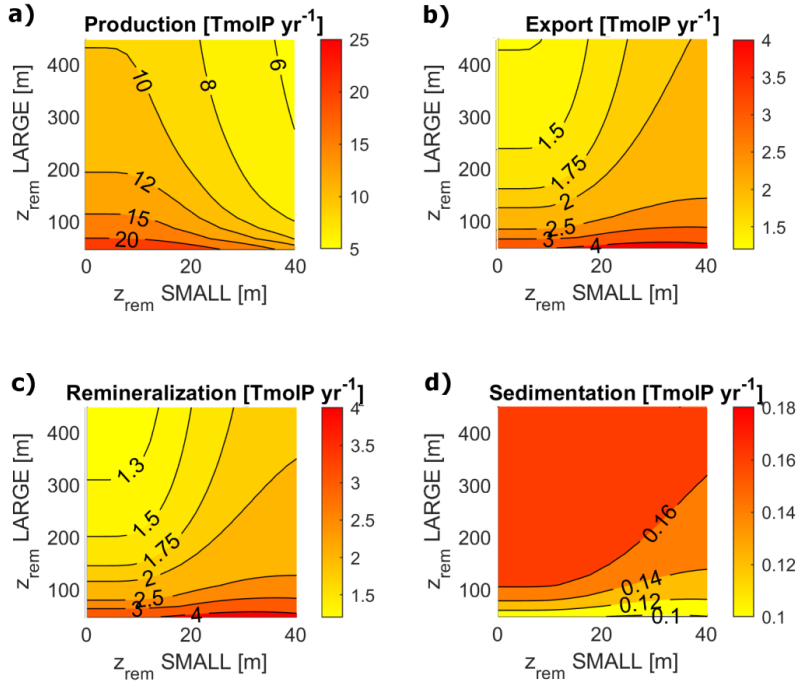


Figure 6: Biological pump fluxes in P units for the entire ocean for varying z_{rem}^S and z_{rem}^L: (a) P_{org} surface production; (b) P_{org} export through the euphotic layer depth; (c) P_{org} deep remineralization in both water column and sediments; (d) P_{org} sedimentation at the ocean bottom.

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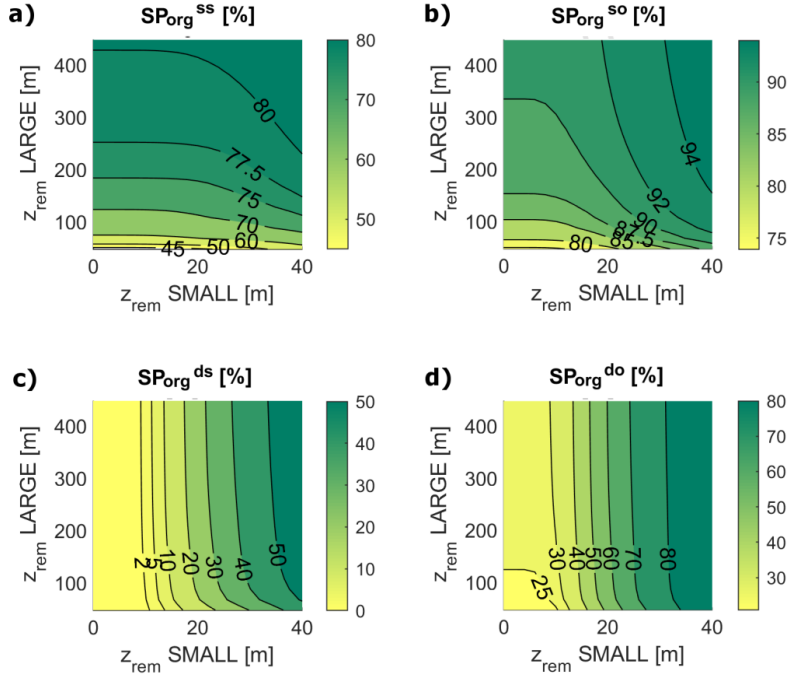


Figure 7: Small P_{org} (SP_{org}) fraction after coagulation in the surface and at depth for varying z_{rem}^{S} and z_{rem}^{L}: (a) surface shelf sea, ss; (b) surface open ocean, so; (c) deep shelf sea, ds; (d) deep open ocean, do.

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Appendix A: Equations

A.1 Air-sea gas exchange of oxygen

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

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

A.2 Surface shelf sea (ss)

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

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

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

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

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

$${VExp_SP_{org}}^{ss} = ({SP_{org}}^{ss} - LatExp^{ss}) \cdot (exp(-(\Delta Z_{eu}/2)/z^S_{rem}) + Mix_{vs}/V^{ss}) \quad \text{(A8)}$$

$${VExp_LP_{org}}^{ss} = {LP_{org}}^{ss} \cdot (exp(-(\Delta Z_{eu}/2)/z^L_{rem}) + Mix_{vs}/V^{ss}) \quad \text{(A9)}$$

$$\boldsymbol{\frac{dP^{ss}}{dt}} = P_{in} \cdot (1 - \mathcal{P}_{open})/V^{ss} + (Upw \cdot (P^{ds} - P^{ss}) + Mix_{ls} \cdot (P^{so} - P^{ss}) + Mix_{vs} \cdot (P^{ds} - P^{ss}))/V^{ss} + - \left(\mathrm{VExp_{SP_{org}}}^{ss} + \mathrm{VExp_{LP_{org}}}^{ss}\right) \quad \text{(A10)}$$

$$AirSea^{ss} = K_W \cdot (O^{at}/K_{Henri} - O^{ss}) \cdot (A_{ocean} \cdot \mathcal{P}_{shelf})/V^{ss} \quad \text{(A11)}$$

$$OProd^{ss} = OP_{Red} \cdot \left(VExp_{SP_{org}}{}^{ss} + VExp_{LP_{org}}{}^{ss}\right) \quad \text{(A12)}$$

$$\boldsymbol{\frac{dO^{ss}}{dt}} = \left(Upw \cdot (O^{ds} - O^{ss}) + \mathrm{Mix}_{ls} \cdot (O^{so} - O^{ss}) + \mathrm{Mix}_{vs} \cdot (O^{ds} - O^{ss})\right)/V^{ss} + AirSea^{ss} + OProd^{ss} \quad \text{(A13)}$$

https://doi.org/10.5194/gmd-2019-182
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Geoscientific Model Development Discussions

A.3 Deep shelf sea (ds)

$$V^{ds} = \Delta Z_{ds} \cdot A_{ocean} \cdot \mathcal{P}_{shelf} \quad \text{(A14)}$$

$$VInp_SP_{org}{}^{ds} = VExp_SP_{org}{}^{ss} \cdot (V^{ss}/V^{ds}) \quad \text{(A15)}$$

$$SP_{org}{}^{ds} = VInp_SP_{org}{}^{ds} - cg_r \cdot (VInp_SP_{org}{}^{ds})^2 \quad \text{(A16)}$$

$$LP_{org}{}^{ds} = VExp_LP_{org}{}^{ss} \cdot (V^{ss}/V^{ds}) + cg_r \cdot (VInp_SP_{org}{}^{ds})^2 \quad \text{(A17)}$$

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

$$Rem_SP_{org}{}^{ds} = (SP_{org}{}^{ds} - LatExp^{ds}) \cdot (1 - exp(-\Delta Z_{ds}/z^S_{rem})) \quad \text{(A19)}$$

$$Rem_LP_{org}{}^{ds} = LP_{org}{}^{ds} \cdot (1 - exp(-\Delta Z_{ds}/z^L_{rem})) \quad \text{(A20)}$$

$$Rem_SedP_{org}{}^{ds} = rm_r \cdot SedP_{org}{}^{s}/\Delta Z_{ds} \cdot (O^{ds}/(O^{ds} + K_O)) \quad \text{(A21)}$$

$$\frac{\boldsymbol{dP^{ds}}}{\boldsymbol{dt}} = (Upw \cdot (P^{do} - P^{ds}) + Mix_{ld} \cdot (P^{do} - P^{ds}) + Mix_{vs} \cdot (P^{ss} - P^{ds}))/V^{ds} + \\ + \left(Rem_SP_{org}{}^{ds} + Rem_LP_{org}{}^{ds} + Rem_SedP_{org}{}^{ds}\right) \quad \text{(A22)}$$

$$AerRem^{ds} = OP_{Red} \cdot (Rem_SP_{org}{}^{ds} + Rem_LP_{org}{}^{ds}) \cdot (O^{ds}/(O^{ds} + K_O)) \quad \text{(A23)}$$

$$SedRemO^{ds} = OP_{Red} \cdot Rem_SedP_{org}{}^{ds} \quad \text{(A24)}$$

$$\frac{\boldsymbol{dO^{ds}}}{\boldsymbol{dt}} = (Upw \cdot (O^{do} - O^{ds}) + Mix_{ld} \cdot (O^{do} - O^{ds}) + Mix_{vs} \cdot (O^{ss} - O^{ds}))/V^{ds} - AerRem^{ds} - SedRem^{ds} \quad \text{(A25)}$$

A.4 Surface open ocean (so)

$$V^{so} = \Delta Z_{eu} \cdot A_{ocean} \cdot (1 - \mathcal{P}_{shelf}) \quad \text{(A26)}$$

$$Prod^{so} = P_{eff} \cdot (P^{so}/(P^{so} + K_P)) \cdot P^{so} \quad \text{(A27)}$$

$$LatInp^{so} = SP_{org}{}^{ss} \cdot (Upw + Mix_{ls})/V^{so} \quad \text{(A28)}$$

$$SP_{org}{}^{so} = (Prod^{so} + LatInp^{so}) - cg_r \cdot (Prod^{so} + LatInp^{so})^2 \quad \text{(A29)}$$

$$LP_{org}{}^{so} = cg_r \cdot (Prod^{so} + LatInp^{so})^2 \quad \text{(A30)}$$

$$VExp_SP_{org}{}^{so} = SP_{org}{}^{so} \cdot (exp(-(\Delta Z_{eu}/2)/z^S_{rem}) + Mix_{vo}/V^{so}) \quad \text{(A31)}$$

$$VExp_LP_{org}{}^{so} = LP_{org}{}^{so} \cdot (exp(-(\Delta Z_{eu}/2)/z^L_{rem}) + Mix_{vo}/V^{so}) \quad \text{(A32)}$$

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Preprint. Discussion started: 14 August 2019
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Geoscientific Model Development Discussions

$$\frac{dP^{so}}{dt} = P_{in} \cdot \mathcal{P}_{open}/V^{ss} + (Upw \cdot (P^{ss} - P^{so}) + Mix_{ls} \cdot (P^{ss} - P^{so}) + Mix_{vo} \cdot (P^{do} - P^{so}))/V^{so} + \\ - \left(VExp_SP_{org}{}^{so} + VExp_LP_{org}{}^{so}\right)$$

(A33)

$$AirSea^{so} = K_W \cdot (O^{at}/K_{Henri} - O^{so}) \cdot (A_{ocean} \cdot (1 - \mathcal{P}_{shelf}))/V^{so} \quad \text{(A34)}$$

$$OProd^{so} = OP_{Red} \cdot \left(VExp_SP_{org}{}^{so} + VExp_LP_{org}{}^{so}\right) \quad \text{(A35)}$$

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

(A36)

A.5 Deep open ocean (do)

$$V^{do} = \Delta Z_{do} \cdot A_{ocean} \cdot (1 - \mathcal{P}_{shelf}) \quad \text{(A37)}$$

$$VInp_SP_{org}{}^{do} = VExp_SP_{org}{}^{so} \cdot (V^{so}/V^{do}) \quad \text{(A38)}$$

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

$$SP_{org}{}^{do} = (VInp_SP_{org}{}^{do} + LatInp^{do}) - cg_r \cdot (VInp_SP_{org}{}^{do} + LatInp^{do})^2 \quad \text{(A40)}$$

$$LP_{org}{}^{do} = VExp_LP_{org}{}^{so} \cdot (V^{so}/V^{do}) + cg_r \cdot (VInp_SP_{org}{}^{do} + LatInp^{do})^2 \quad \text{(A41)}$$

$$Rem_SP_{org}{}^{do} = SP_{org}{}^{do} \cdot (1 - exp(-\Delta Z_{do}/z^{S}_{rem})) \quad \text{(A42)}$$

$$Rem_LP_{org}{}^{do} = LP_{org}{}^{do} \cdot (1 - exp(-\Delta Z_{do}/z^{L}_{rem})) \quad \text{(A43)}$$

$$Rem_SedP_{org}{}^{do} = rm_r \cdot SedP_{org}{}^{o}/\Delta Z_{do} \cdot (O^{do}/(O^{do} + K_O)) \quad \text{(A44)}$$

$$\frac{dP^{do}}{dt} = (Upw \cdot (P^{so} - P^{do}) + Mix_{ld} \cdot (P^{ds} - P^{do}) + Mix_{vo} \cdot (P^{so} - P^{do}))/V^{do} + \\ + \left(Rem_SP_{org}{}^{do} + Rem_LP_{org}{}^{do} + Rem_SedP_{org}{}^{do}\right)$$

(A45)

$$AerRem^{do} = OP_{Red} \cdot (Rem_SP_{org}{}^{do} + Rem_LP_{org}{}^{do}) \cdot (O^{do}/(O^{do} + K_O)) \quad \text{(A46)}$$

$$SedRemO^{do} = OP_{Red} \cdot Rem_SedP_{org}{}^{do} \quad \text{(A47)}$$

$$\frac{dO^{do}}{dt} = (Upw \cdot (O^{so} - O^{do}) + Mix_{ld} \cdot (O^{ds} - O^{do}) + Mix_{vo} \cdot (O^{so} - O^{do}))/V^{do} - AerRem^{do} \\ - SedRem^{do}$$

(A48)

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Preprint. Discussion started: 14 August 2019
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Geoscientific Model Development Discussions

A.6 Shelf sea sediments (s)

$$SedFlx^{s} = \left(\left({SP_{org}}^{ds} - LatExp^{ds} \right) \cdot exp(-\Delta Z_{ds} / z_{rem}^{S}) + {LP_{org}}^{ds} \cdot exp(-\Delta Z_{ds} / z_{rem}^{L}) \right) \cdot \Delta Z_{ds} \quad \text{(A49)}$$

$$CaPform^{s} = CaP_{r} \cdot ({SedP_{org}}^{s})^{2} \quad \text{(A50)}$$

$$\frac{\boldsymbol{d{SedP_{org}}^{s}}}{\boldsymbol{dt}} = SedimFlx^{s} - CaPform^{s} - {Rem_SedP_{org}}^{ds} \cdot \Delta Z_{ds} \quad \text{(A51)}$$

A.7 Open ocean sediments (o)

$$SedFlx^{o} = \left(\left({SP_{org}}^{do} - LatExp^{do} \right) \cdot exp(-\Delta Z_{ds} / z_{rem}^{S}) + {LP_{org}}^{do} \cdot exp(-\Delta Z_{ds} / z_{rem}^{L}) \right) \cdot \Delta Z_{do} \quad \text{(A52)}$$

$$CaPform^{o} = CaP_{r} \cdot ({SedP_{org}}^{o})^{2} \quad \text{(A53)}$$

$$\frac{\boldsymbol{d{SedP_{org}}^{o}}}{\boldsymbol{dt}} = SedimFlx^{o} - CaPform^{o} - {Rem_SedP_{org}}^{do} \cdot \Delta Z_{do} \quad \text{(A54)}$$

A.8 Atmosphere (at)

$$AirSea^{at} = (AirSea^{ss} + AirSea^{so}) / (Mol_{atmo} \cdot 10^{3}) \quad \text{(A55)}$$

$$AnaRem^{ds} = OP_{Red} \cdot ({Rem_SP_{org}}^{ds} + {Rem_LP_{org}}^{ds}) \cdot (1 - O^{ds} / (O^{ds} + K_{O})) \quad \text{(A56)}$$

$$AnaRem^{do} = OP_{Red} \cdot ({Rem_SP_{org}}^{do} + {Rem_LP_{org}}^{do}) \cdot (1 - O^{do} / (O^{do} + K_{O})) \quad \text{(A57)}$$

$$AnaRem^{at} = (AnaRem^{ds} \cdot V^{ds} + AnaRem^{do} \cdot V^{do}) / (Mol_{atmo} \cdot 10^{3}) \quad \text{(A58)}$$

$$OxyWeath = W_{0} \cdot \sqrt{O^{at} / Omix_{0}} / (Mol_{atmo} \cdot 10^{3}) \quad \text{(A59)}$$

$$\frac{\boldsymbol{dO^{at}}}{\boldsymbol{dt}} = -AirSea^{at} - AnaRem^{at} - OxyWeath \quad \text{(A60)}$$

https://doi.org/10.5194/gmd-2019-182
Preprint. Discussion started: 14 August 2019
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Geoscientific Model Development Discussions

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