Modelling the Life-Environment Interface in Ancient Shelf Seas

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This work was funded via a doctoral training grant awarded as part of the UKRI AI Centre for Doctoral Training in Environmental Intelligence (UKRI grant number EP/S022074/1).

Model Scale and Stability Challenges

Co-evolution of life and environment is a dynamic system of feedbacks. Interplays between life and redox in shelf seas have been fundamental to origination and extinction, determining the ecospace and energetics available to biota.

Scale Bidirectional effects of biota and the environment need to be integrated into the same models to capture the dynamics at the redox boundary. Using the PALEO approach we construct a model to target the redox boundary and interactions critical to ecosystem evolution. Biological populations modelled by their functional ecology can help unify previous approaches to modelling ecological networks, the biological pump, and sediment transport.

Stability Evolving ecosystems have become increasingly diverse and complex. Integrating ecological models into environmental models is creating new avenues for reducing degrees of freedom and exploring parameter space for stable communities by connecting ecological modules back to Earth system processes and mass-budgets.

Early Evolution and Ecosystem Engineers

The shelf sea model can test a number of hypotheses related to the co-evolution of life and oxygenation of the ocean and ocean floor in the Neoproterozoic and Cambrian.

Hypothesis 1:
Sponge filter-feeding selected for larger plankton causing ocean oxygenation
Early metazoan evolution coincided with major changes to ocean redox. Lenton et al (2014) suggested that evolution of filter-feeding sponges exerted a size-selective pressure on eukaryotic plankton, increasing export of organics to the sediment surface. Moving oxygen demand to deeper waters could create a runaway feedback oxygenating the ocean. The shelf sea model supports multiple size classes of plankton, allowing the efficiency of this mechanism to be tested.

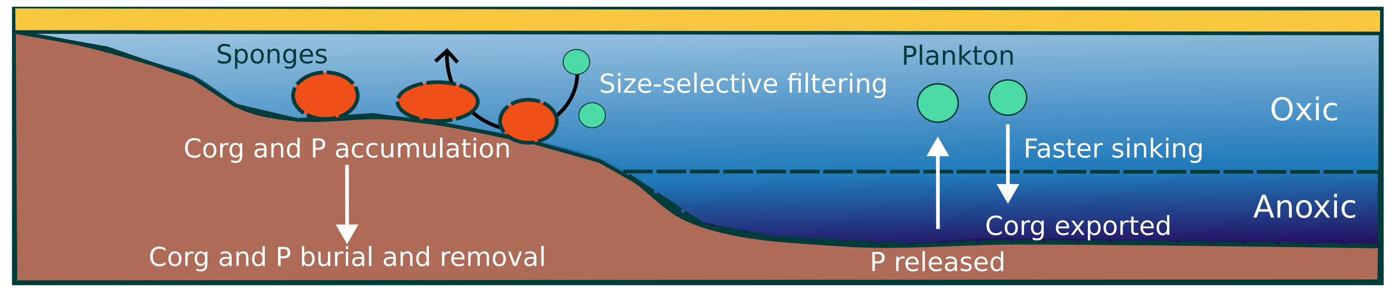

Diagram 1: The effect of sponge evolution on the P and O cycles, adapted from Lenton et al (2014).

Hypothesis 2:
The Agronomic Revolution caused a runaway feedback in the P-cycle
During the Cambrian Explosion burrowing organisms invaded the sediment. The initial burrowing activity increased sediment irrigation and connection with overlying oxic waters, creating a positive feedback with the phosphorous and oxygen cycles. Progressive deepening of the redoxcline then allowed for deeper biotic invasion.

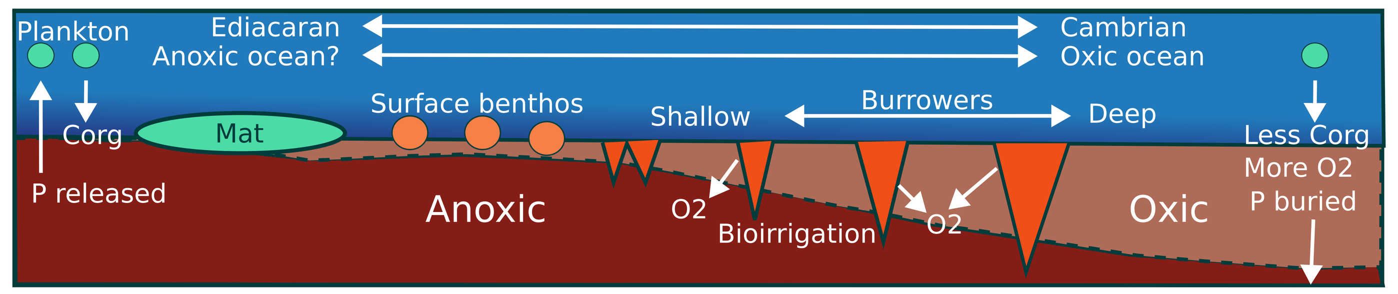

Diagram 2: Deepening of the redoxcline during the Cambrian Substrate Revolution.

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Configurable Shelf Sea Column Model

Abiotic

Atmosphere
Single cell
O2

Ocean Surface
Surface area
Gas exchange

Light
Advection
Sinking

Ocean
Column of volume cells
S2P3-R Marsh et al (2015)
P O2 H2S SO4 CH4
Plankton

Ocean Floor
Surface area
Particulate & solute exchange
Benthos

Sediment
Column of volume cells
Transport Boudreau (1996)
P O2 H2S SO4 CH4 Corg
Burrowers
Microbes

Biotic

Plankton
Phosphorus — Phytoplankton — Zooplankton
P → P0 → Z0
ϕ
P → P1 → Z1
Size-structured food chains

Benthic sessile microorganisms
Consume sinking plankton
Heterotroph characteristics
O2 and nutrient-dependent growth

Benthic sessile macroorganisms
Consume sinking plankton
Movement-driven capture rate
O2 and nutrient-dependent growth

Burrowing deposit feeders
Increasing irrigation
Consume buried Corg
Vertical burrows only
Bioirrigation and diffusivity proportional to population
O2 and nutrient-dependent growth
Living maintain depth, dead buried

Sediment microbes
Replace reactive-continuum model
Consume organics from ocean column
O2 and nutrient-dependent growth
Respiration generates redox profile

Growth

Micro-growth

Microorganisms in diffusive regimes grow as in Armstrong (1994), but here phosphorus is used as the nutrient.

For nutrient assimilation in autotrophs:

$$\frac{\partial P_i}{\partial dt} = P_i(\mu_{max,i}\frac{S}{K_{S,i}+S} - \lambda_i - Z_i\frac{H_{max,i}}{K_{P,i}})$$

For feeding in heterotrophs:

$$\frac{\partial Z_i}{\partial dt} = Z_i(\gamma_i\frac{H_{max,i}}{K_{P,i}}P_i - \delta_i)$$

S nutrient concentration, mmol N m^{-3}; P_i population of plankton, mmol N m^{-3}; Z_i population of zooplankton, mmol N m^{-3}; $\mu_{max,i}$ maximum phytoplankton, growth rate d^{-1}; λ_i plankton growth, mmol N m^{-3}; $H_{max,i}$ maximum zooplankton harvest rate, mmol P d^{-1}; $K_{P,i}$ zooplankton full-saturation constant for harvest and growth, mmol P m^{-3}; γ_i zooplankton growth efficiency, dimensionless; δ_i intrinsic zooplankton loss rate, d^{-1}

Macro-growth

Macrobiology growth can be conceptualized as a flux of nutrient into the biological reservoir, such that:

***Growth** = movement rate of the organism x size of organism x prey concentration x capture efficiency x assimilation efficency*

For sessile organisms, such as filter feeders, the movement is that of the water relative to the organism, conceptually the same as the organism through the water. For example for sponges:

***Sponge growth** = sponge pump rate x sponge concentration x POC & plankton concentration x capture efficiency x assimilation efficiency*

Schematic 1: The shelf sea model explores redox-nutrient-biota dynamics in the evolutionarily critical shelf sea setting. Organisms are represented as concentrations of phosphorus, and their feeding and respiration alter the flux of phosphorous and oxygen through the ecosystem, forming feedbacks affecting ocean and sediment oxygen profiles and burial rates. The size-structured ocean column organic particles sink and are remineralized, or transferred to the sediment, replacing the reactive continuum model parameterized from modern data with explicit organic reservoirs which are metabolized by microbial activity. The redox profile is directly generated by the respiration of the biotic populations and bioirrigation and bioturbation parameters scaled to the burrowing population.

Managing Scale for Tractable Models

The **PALEO framework**'s approach to managing scale is three-fold:

1. Use process-based modelling to represent phenomena. Using energy laws, physics, ecological basics or universal principles can help limit the number of unknowns and scales the parametrization required to the data available.

2. Exploit timescale separation to abstract out variables of shorter or longer timescales than the phenomenon of interest.

3. Build a hierarchy of tractable models to prioritize important components while reducing dimensionality, without losing the conceptual and numerical connection to the whole Earth system.

Single NPZ Food Chain Model Output

Simple process-based ecological representations of a single nutrient-phytoplankton-zooplankton food chain and the reduced dimensionality of the environmental shelf sea model in **Schematic 1** are sufficient to produce a plausible shelf sea seasonal pattern for phosphorus, oxygen and the biota, shown in **Figures 2-4**.

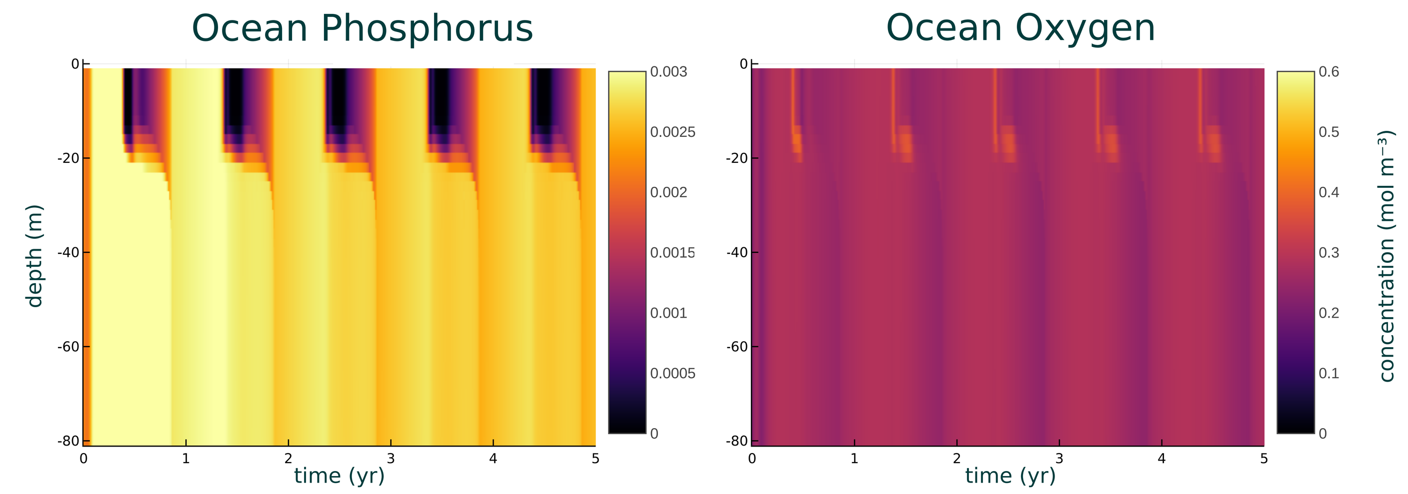

Figure 2a,b: As the seasonal solar energy flux increases, the light-dependent phytoplankton begin to consume phosphorous and produce oxygen.

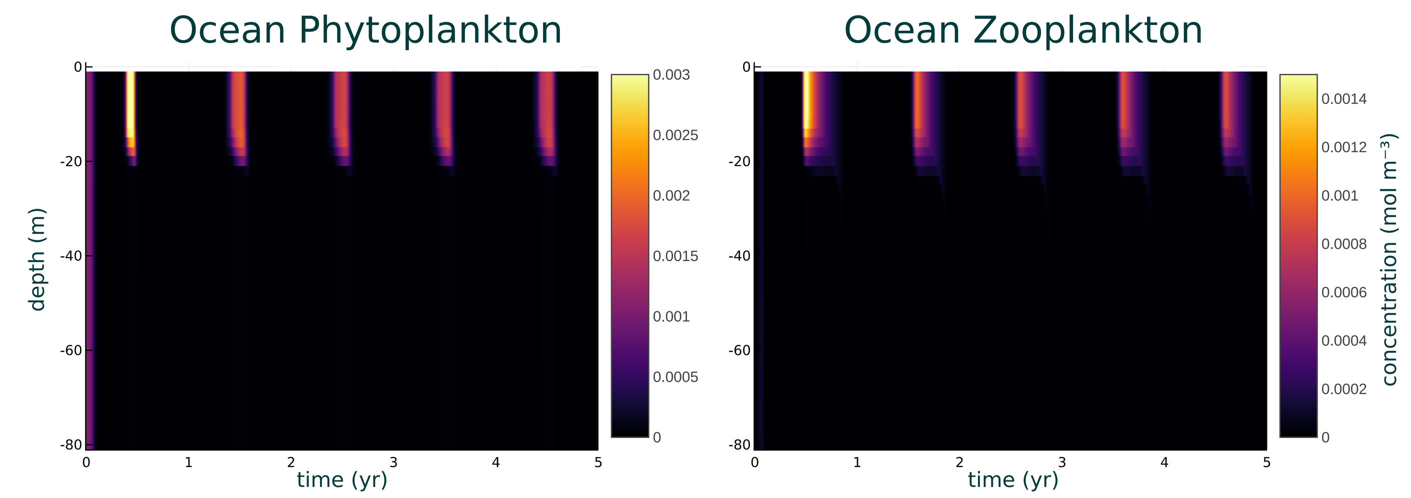

Figure 3a,b: Zooplankton feed on the phytoplankton, reducing their population and growing their own.

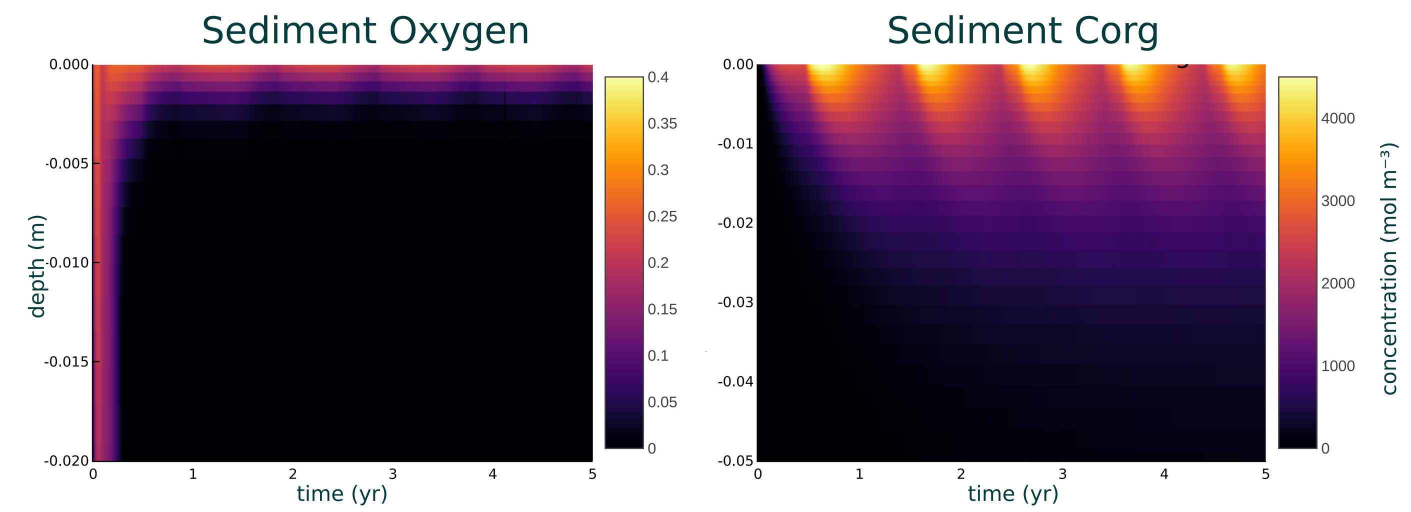

Figure 4a,b: The decaying organics sink to the bottom, feeding the sessile benthos and consuming oxygen. Organic carbon which is not consumed or remineralized is buried in the sediment.