ECOLOGICAL CONTROL OF SUBTROPICAL NUTRIENT CONCENTRATIONS

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1. INTRODUCTION

We use simple theoretical constructs and three-dimensional numerical simulations to examine the biogeography of the oceans. We examine the interplay between ecosystem structure and biogeochemical cycles, particularly ecological controls on nutrient concentrations.

- A global coupled physical-biogeochemistry-ecosystem ocean model has been constructed where phytoplankton communities "self-assemble" from a wide set of potentially viable cell types (Follows et al., 2007). This model produces plausible ecosystem biogeography.

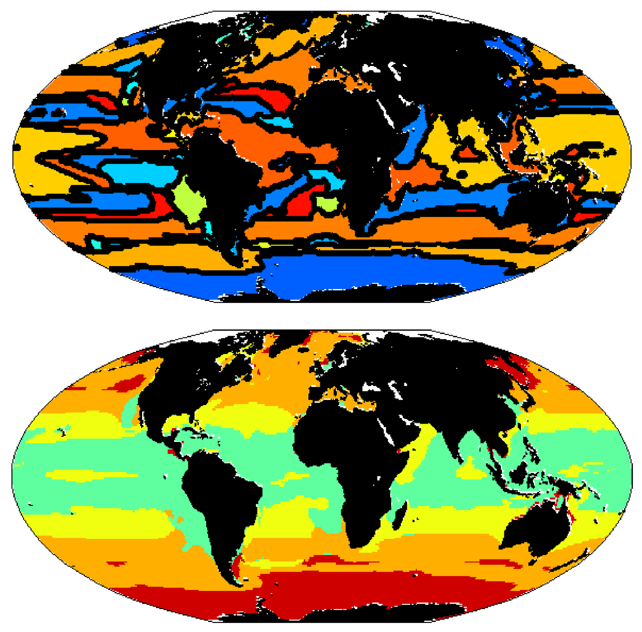

Figure 1 *Multiple-Resource Experiment.* **(top)** *Emergent biogeographical provinces, defined by most dominant species, reminiscent of Longhurst (1995).* **(bottom)** *Biogeography of four major functional groups: (i) Diatom-analogs (red), (ii) other large phytoplankton (orange), (iii)* Prochlorococcus*-analogs (green), and (iv) other small phytoplankton (yellow-green).*

- We use this numerical framework to investigate the emergent biogeography and controls on biogeochemistry. Theoretical constructs, in particular "Resource Control Theory" (Tilman, 1977) can aid us in this investigation.

2. ECOLOGICAL FRAMEWORK

Consider a simple system where many phytoplankton (P_j) are nourished by nutrient (N) resupplied at rate S. Phytoplankton are lost at rate m, and have physiology controlled by growth rate (μ_j) and nutrient half-saturation (K_{N_j}).

$$\frac{dN}{dt} = -\sum_j \mu_j \frac{N}{N+K_{N_j}} P_j + S \qquad (1)$$

$$\frac{dP_j}{dt} = \mu_j \frac{N}{N+K_{N_j}} P_j - m_j P_j \qquad (2)$$

1) In steady state ("Resource Control Theory"):

$$N_j^* = \frac{K_{N_j} m_j}{\mu_j - m_j} = R_j^* \qquad (3)$$

$$\sum m_j P_j^* = S \qquad (4)$$

- Nutrients are drawn down to the lowest R^*, organisms with higher R^* can not compete (**K-selection**); Coexistence can occur if phytoplankton have the same R^*.
- Nutrient concentration is determined by phytoplankton physiology and losses; Phytoplankton concentrations are controlled by their loss rates and the supply of nutrient.

2) At beginning of spring in highly seasonal region: Growth rate matters most (**r-selection**).

$$\frac{1}{P}\frac{dP}{dt} \sim \mu \qquad (5)$$

3. NUMERICAL SIMULATIONS

- Model simulations are initialized with 78 phytoplankton types with assorted set of growth parameters, and 2 grazers (Follows et al., 2007 with minor modifications).
- The biogeochemical-ecosystem is embedded in the circulation states estimates provided by the ECCO-GODAE consortium (Wunsch and Heimbach, 2007).
- We consider 2 experiments:
  - **Single Resource Case**. One nutrient, phytoplankton are divided into two groups. K-strategy with low R^* (low K_N, high μ) and one has higher R^* (high μ, high K_N).
  - **Multiple Resource Case**. N, P, Si and Fe cycling. Phytoplankton growth traits are randomly assigned from within reasonable ranges.

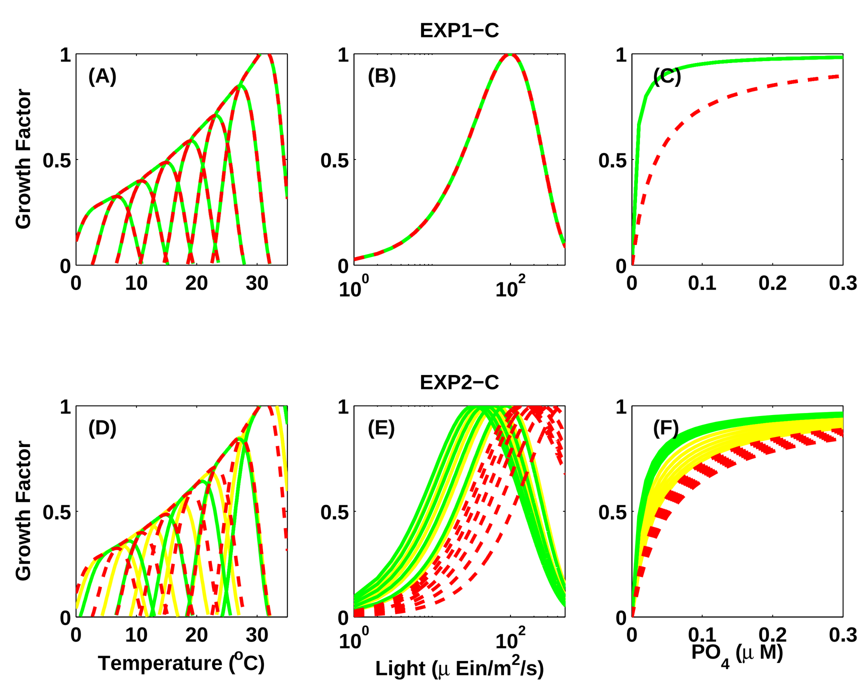

Figure 2. *Growth $\mu = \mu_{max}\gamma_T\gamma_I\gamma_N$ is function of temperature (γ_T), light (γ_I), and nutrients (γ_N).* **(top)** *Single Resource Case,* **(bottom)** *Multiple Resource Case. Green and yellow: K-strategy phytoplankton types with low half-saturation constants and low μ_{max}. Red: r-strategy phytoplankton types with high μ_{max} and high half-saturation constants. Green: small phytoplankton that cannot use nitrate (*Prochlorococcus *analogs).*

4. SINGLE RESOURCE CASE

We use this simplified model as an illustrative tool for our approach, before looking at the more complex model.

4.1. Which type lives where?

- r-strategy types dominate in high latitudes: high seasonality and high nutrients; K-strategy types dominate in the low and mid latitudes.

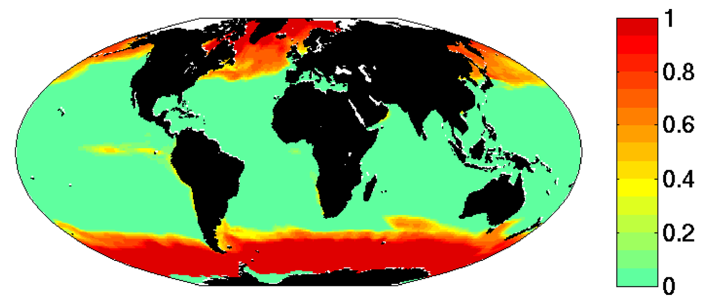

Figure 3 *Single Resource case. Fraction of biomass in r-strategy types relative to total biomass.*

4.2. Ecological Nutrient Control

- Eq. 3 suggest that nutrient concentrations will be affected by changes to the phytoplankton physiology.
- In sensitivity studies we repeat the simulation, but change K_N: double and half the value in the control run.
- In most of region dominated by K-strategy types, nutrient concentrations can be controlled by the phytoplankton physiology (Eq. 3); Phytoplankton concentrations however remain almost identical to the control run (Eq. 4).

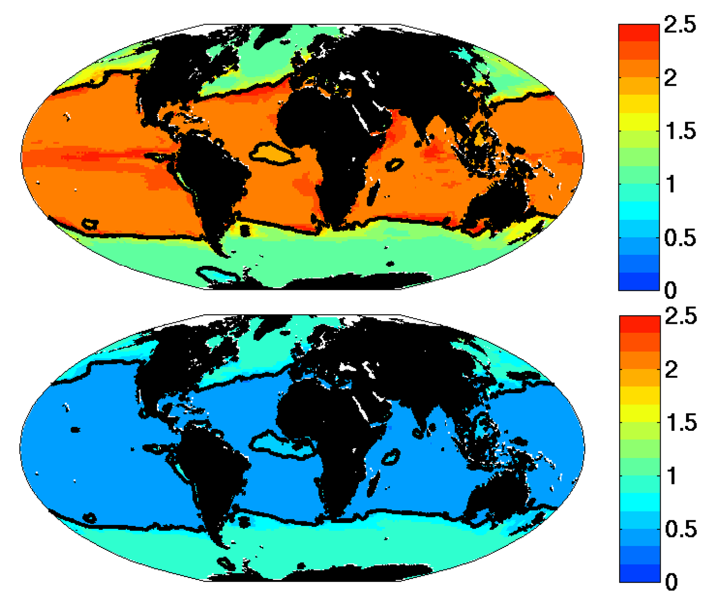

Figure 4 *Single Resource Case. Ratio of macro-nutrients of sensitivity experiment to control case.* **(top)** *K_N doubled,* **(bottom)** *K_N halved. Contours at .5 (sensitivity study has half the macro-nutrient) and 2 (sensitivity study has double the macro-nutrients).*

4.3. Biogeography

- Nutrients are ecologically controlled in relatively stable regimes (mixed layer depth annual range $<$ 250m).

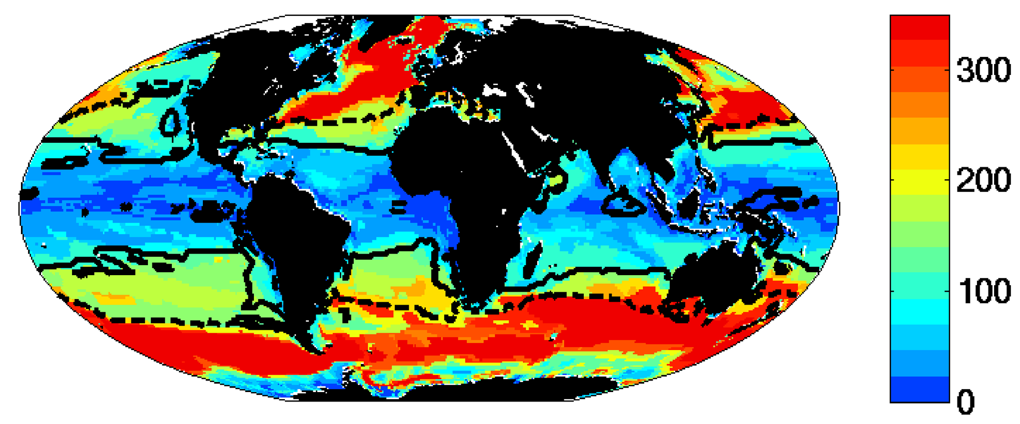

Figure 5 *Annual range of mixed layer depth. Dashes contour indicates where macro-nutrient concentration can be predicted by resource control theory (see Fig. 4). Solid line indicates the region where the Prochlorococcus-analogs dominate in the multiple resource case.*

5. MULTIPLE RESOURCE CASE

How well does the theory hold for a more realistic simulation? We consider an experiment with the cycling of N, P, Si, Fe and more strategy types of phytoplankton (e.g additional nutrient limitation, differing light requirement, differing grazing potential).

5.1. Which types live where?

- Transition between regimes is gentler than in Single Resource Case. (see Fig. 2).

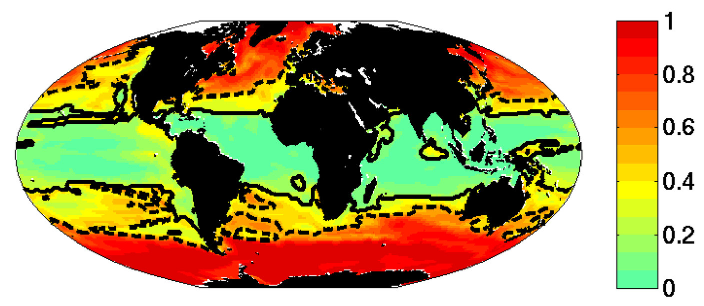

Figure 6 *Multiple Resource case. Fraction of biomass in "large" (faster growing) relative to total biomass (compare to Fig. 3). Dashed line indicates the 0.5 contour. Solid line indicates the region where the Prochlorococcus-analogs dominate.*

5.2 Ecological Nutrient Control

- In sensitivity studies we double and halve K for all nutrients.
- Most limiting nutrient in the low and mid latitudes is controlled by the phytoplankton assemblage:
- Iron in the Equatorial Pacific and inorganic nitrogen elsewhere.

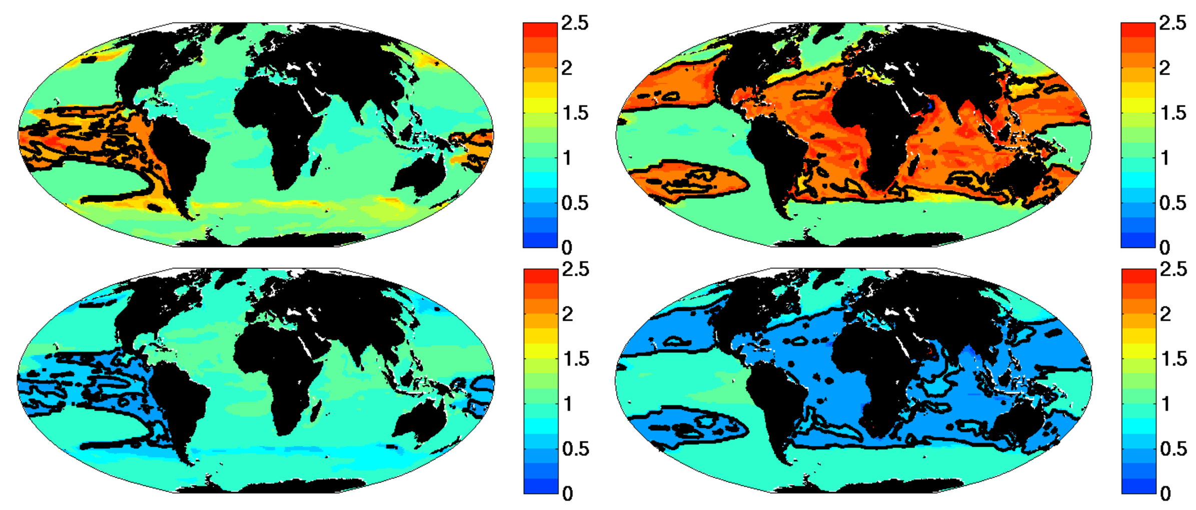

Figure 7 *Multiple Resource Case: Ratio of* **(left)** *Fe,* **(right)** *Inorganic nitrogen (NO_3+NO_2+NH_4) of sensitivity experiment to control case.* **(top)** *K_N doubled,* **(bottom)** *K_N halved.*

5.3 Biogeography

- Region where limiting nutrient appears controlled by the phytoplankton physiology is qualitatively similar to Single Resource Case (annual mixed layer depth range $<$ 250m, Fig. 5).
- *Prochlorococcus*-analogs have the lowest R^*, but are also unable to utilize nitrate. These dominate (Fig. 1) in most stable sub-region (annual mixed depth range $<$ 100m, Fig. 5). Annual temperature and PAR ranges are also small here.

6. SUMMARY

- The r and K strategy types dominate in the regions we would expect: low nutrient requirements (K) in the low/mid latitude relatively low seasonal regions, and high growth rates (r) in the highly seasonal regions where nutrients are also high.
- In regions of relative stable physical environment, phytoplankton physiology has a important role in setting the biogeochemical environment.
- Links to ecological theory have helped us better understand our numerical simulation ... and potentially the real marine environment.

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