

Modelling the Vertical Dynamics of Phytoplankton Populations in Freshwater Systems

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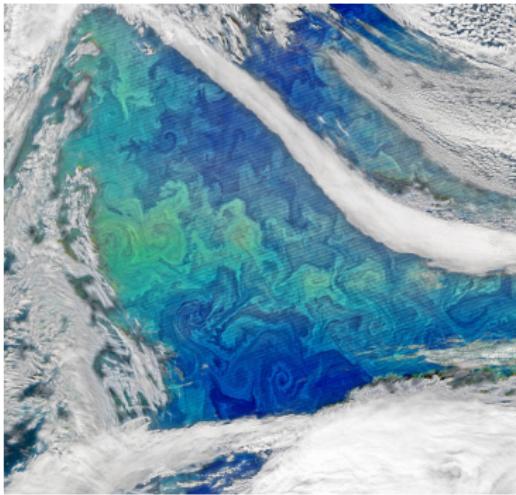
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Introduction: What are Phytoplankton?



Phytoplankton bloom viewed from space¹

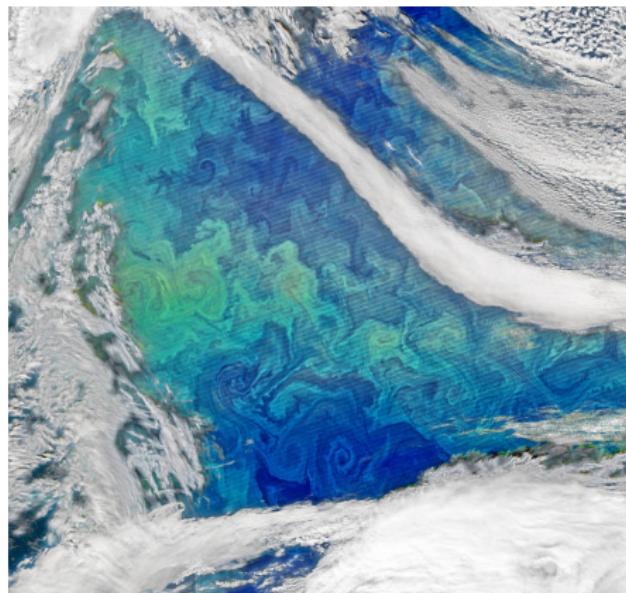
- Phytoplankton are microscopic, photosynthesising organisms at the base of the entire aquatic food web
- The word plankton comes from the Greek word for wandering or drifters
- They are small but incredibly important
- The mechanisms behind phytoplankton population "blooms" are a topic of scientific debate
- It is an area of significant importance in marine conservation policy

¹Photo by Kuring, N for NASA, 2017

Introduction: Why Study Phytoplankton?

They form the foundation for the health of entire aquatic ecosystems:

- Low-populations of phytoplankton in food shortages all the way up the food chain
- Large "blooms" use up all the oxygen in the water, leading to the die-off of marine life
- Some species release toxins which can travel up the food chain and even affect humans, these are named harmful algal blooms or HABs



Phytoplankton bloom viewed from space²

²Photo by Kuring, N for NASA, 2017

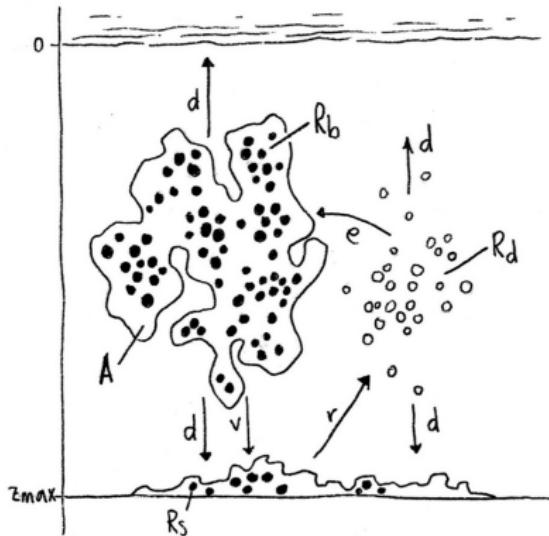
The Model

We study a simple model³ with the following main properties:

- A single species of phytoplankton A relies on a single nutrient R (phosphorus) in a 1-dimensional column of water
- Nutrients cannot escape from the system but are recycled throughout it continuously
- As photosynthesising organisms, plankton growth is limited to shallower water where more light is available - the euphotic zone
- The phytoplankton sink and diffuse helplessly in the water and cannot propel themselves in any direction

³ Jaeger et al (2010) "Physical Determinants of Phytoplankton Production; Algal Stoichiometry; and Vertical Nutrient Fluxes.".

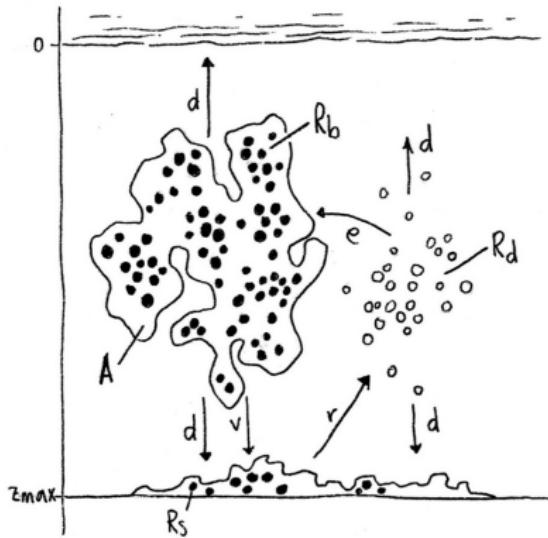
The Model: Nutrient Cycle



The cycle of nutrients can be understood to evolve as follows:

- Dissolved nutrients R_d diffuse up and down in the water at a diffusion rate d
- They are taken in (eaten) by the plankton at a rate ρ and become bound nutrients R_b

The Model: Nutrient Cycle ctd.



- The bound nutrients drift with the plankton "cloud" and also sink with it at a drift rate v
- Nutrients that reach z_{max} become sedimented as R_s and nutrients at z_{max} dissolve back into the water as R_d at a rate r

The system is assumed to be closed for nutrients,

$$\Rightarrow R = R_b + R_d + R_s$$

The Equations

The equations for this model, as proposed by Jaeger et al.⁴ are as follows:

- (i) The main three reaction-advection diffusion equations describing the evolution of plankton A , bound nutrients R_b and dissolved nutrients R_d :

$$\begin{aligned}\frac{\partial A}{\partial t} &= p(I, q)A - I_{bg}A - v \frac{\partial A}{\partial z} + d \frac{\partial^2 A}{\partial z^2} \\ \frac{\partial R_b}{\partial t} &= \rho(q, R_d)A - I_{bg}R_b - v \frac{\partial R_b}{\partial z} + d \frac{\partial^2 R_b}{\partial z^2} \\ \frac{\partial R_d}{\partial t} &= -\rho(q, R_d)A + I_{bg}R_b + d \frac{\partial^2 R_d}{\partial z^2}\end{aligned}$$

Note: the z-axis is inverted here so larger values correspond to deeper depths.

⁴ Jaeger et al (2010) "Physical Determinants of Phytoplankton Production; Algal Stoichiometry; and Vertical Nutrient Fluxes.".

The Equations ctd.

(ii) Ordinary differential equations for light intensity I and sedimented nutrients concentration R_s :

$$I(z) = I_0 \exp \left(- \int_0^z kAdz + k_{bg}z \right)$$

$$\frac{\partial R_s}{\partial t} = vR_b(z_{max}) - rR_s$$

The Equations ctd.

(iii) The growth (p) and nutrient uptake (ρ) functions:

$$p(I, q) = \mu_{max} \left(\frac{q - q_{min}}{q} \right) \frac{I}{h + I}$$

$$\rho(q, R_d) = \rho_{max} \left(\frac{q_{max} - q}{q_{max} - q_{min}} \right) \frac{R_d}{m + R_d}$$

q is the ratio $\frac{R_b}{A}$ and indicates how "well-fed" the plankton is.

Boundary Conditions at Surface

Define J_A , J_{R_b} and J_{R_d} as the convective fluxes of algae, bound and dissolved nutrients,

$$J_A = vA - dA' = 0$$

$$J_{R_b} = vR_b - dR'_b = 0$$

$$J_{R_d} = -dR'_d = 0.$$

- Nutrients and algae can neither enter or leave the water at the surface
- So set the convective fluxes to zero
- We obtain two Robin boundary conditions and one Neumann boundary condition⁵.

⁵as provided in the paper by Jaeger et al. (2010).

Boundary Conditions at z_{max}

- At z_{max} algae and bound nutrients enter the sediment
- So we don't want A and R_b diffusing back out of the z_{max}
- Their net current must a downward drifting current only
- Neumann boundary conditions set the diffusive element of their currents $dA' = dR'_b = 0$ ⁶.

⁶as provided in Jaeger et al. (2010).

Boundary Conditions at z_{max} ctd.

- A Robin boundary condition for R_s and R_d preserves the total concentration of nutrients in the system
- Ensuring the influx current of nutrients into R_s from R_d via diffusion d is equal to the outflux by remineralisation r yields,
$$J_{R_d} = -dR'_d(z_{max}) = -rR_s^7.$$
⁷

⁷Jaeger (2010).

Table of Boundary Conditions

Summarising the boundary conditions,

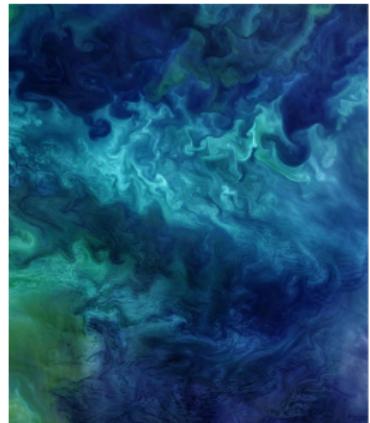
Variable	Surface	z_{max}
A	$vA(0) - dA'(0) = 0$	$A'(z_{max}) = 0$
R_b	$vR_b(0) - dR'_b(0) = 0$	$R'_b(z_{max}) = 0$
R_d	$R'_d(0) = 0$	$rR_s - dR'_d(z_{max}) = 0$
I	$I(0) = I_0$	

Table 1: Boundary conditions, taken from Jaeger et al.⁸

⁸Jaeger (2010).

Turbulence and Light in the Model

- The drifting plankton are unable to swim up into the euphotic zone
- This means they depend entirely on water turbulence (coefficient *d*) for long-term survival
- Turbulence and light intensity emerge as key players in the survival of phytoplankton populations



*Phytoplankton bloom in the Chukchi Sea, June 2018*⁹

⁹Kuring, N for NASA (2017) "Phytoplankton Bloom in the North Atlantic".

Questions

So how do (a) water turbulence and
(b) surface light intensity regulate
phytoplankton populations?

To study this we will find approximate solutions the system of equations and use this to,

- ① run simulations while changing d or I_0
- ② study stationary distributions for different values of d and I_0

Finite Difference Method

- A finite difference method was used to discretise the differential equations
- Time was discretised using the forward Euler method
- Space was discretised using the centered difference approximations for the first and second order derivatives

Finite Difference Method

$$A_z^{t+\Delta t} = A_z^t + \Delta t \left(p(I_z^t, q_z^t) A_z^t - I_{bg} A_z^t - v \frac{A_{z+\Delta z}^t - A_{z-\Delta z}^t}{2\Delta z} + d \frac{A_{z+\Delta z}^t - 2A_z^t + A_{z-\Delta z}^t}{\Delta z^2} \right)$$

$$R_{bz}^{t+\Delta t} = R_{bz}^t + \Delta t \left(\rho(q_z^t, R_{dz}^t) A_z^t - I_{bg} R_{bz}^t - v \frac{R_{bz+\Delta z}^t - R_{bz-\Delta z}^t}{2\Delta z} + d \frac{R_{bz+\Delta z}^t - 2R_{bz}^t + R_{bz-\Delta z}^t}{\Delta z^2} \right)$$

$$R_{dz}^{t+\Delta t} = R_{dz}^t + \Delta t \left(-\rho(q_z^t, R_{dz}^t) A_z^t + I_{bg} R_{bz}^t + d \frac{R_{dz+\Delta z}^t - 2R_{dz}^t + R_{dz-\Delta z}^t}{\Delta z^2} \right)$$

$$R_s^{t+\Delta t} = R_s^t + \Delta t (v R_{bz_{max}}^t - r R_s^t)$$

and the ODE for I is discretised by expressing

$\int_0^z kA dz$ as $\sum_i kA(i)\Delta z$ where $i = 0, \Delta z, 2\Delta z, \dots, z$.

Finite Difference Method: Boundary Conditions

To discretise the boundary conditions the second-order formula for the first derivative is used¹⁰

$$f'(x) = \frac{1}{2h} (-3f(x) + 4f(x + h) - f(x + 2h)) + O(h^2)$$

yielding the discretised boundary conditions,

Variable	Surface	z_{max}
A	$A_0 = \frac{d}{2v\Delta z + 3d} (4A_1 - A_2)$	$A_M = \frac{1}{3}(-A_{M-2} + 4A_{M-1})$
R_b	$R_{b0} = \frac{d}{2v\Delta z + 3d} (4R_{b1} - R_{b2})$	$R_{bM} = \frac{1}{3}(-R_{bM-2} + 4R_{bM-1})$
R_d	$R_{d0} = \frac{1}{3}(4R_{d1} - R_{d2})$	$R_{dM} = \frac{1}{3d} (4dR_{dM-1} - dR_{dM-2} + 2r\Delta z R_s)$
I	$I(0) = I_0$	

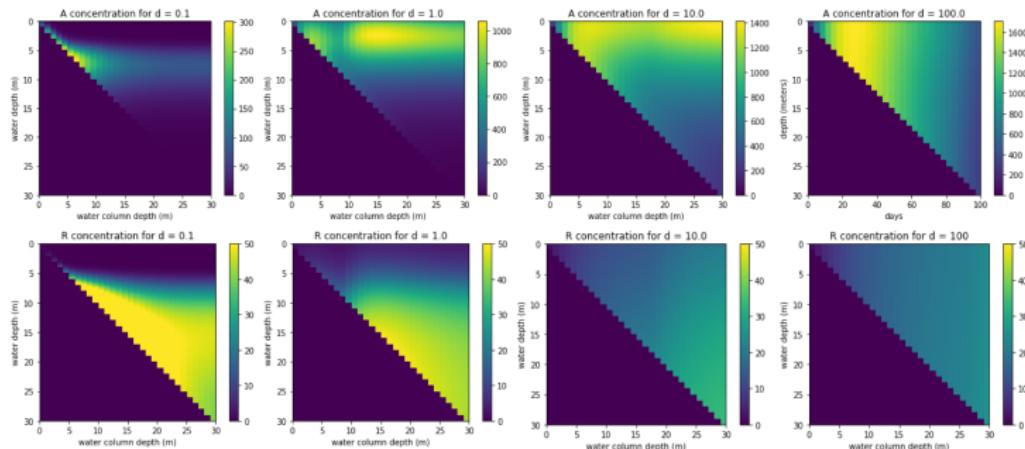
¹⁰Sauer; T. (2012) "Numerical analysis" (2nd ed.).

Turbulence

- How does turbulence generally affect the distribution of a phytoplankton population?
- Are there values that don't support life?
- Does water column depth affect this?

Heatmaps in Depth-Turbulence Space

Stationary distributions of the phytoplankton A and total nutrient R concentrations for $d = \{0.1, 1, 10, 100\}$ at different lake depths are shown here,¹¹

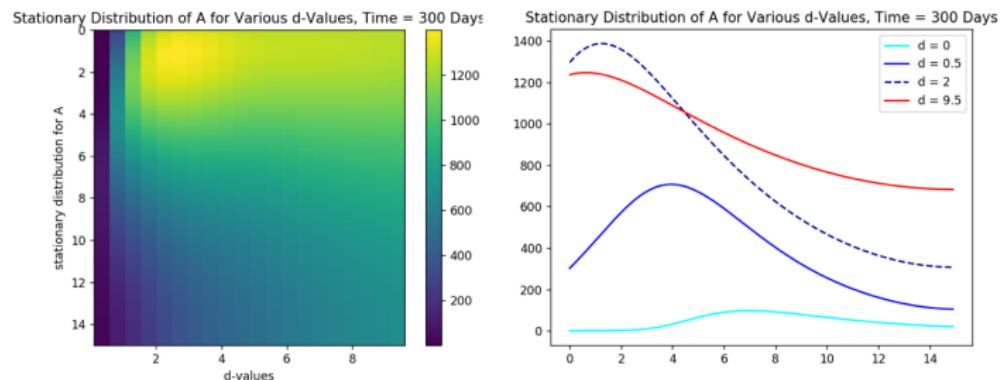


- At low turbulence populations thrive near the surface in the euphotic zone
- At high turbulence the water is well-mixed
- Light and lake depth seem to have different importances depending on d

¹¹These heatmaps reproduce the work of Jaeger et al. (2010).

Changing Turbulence for Lake of Depth 15m

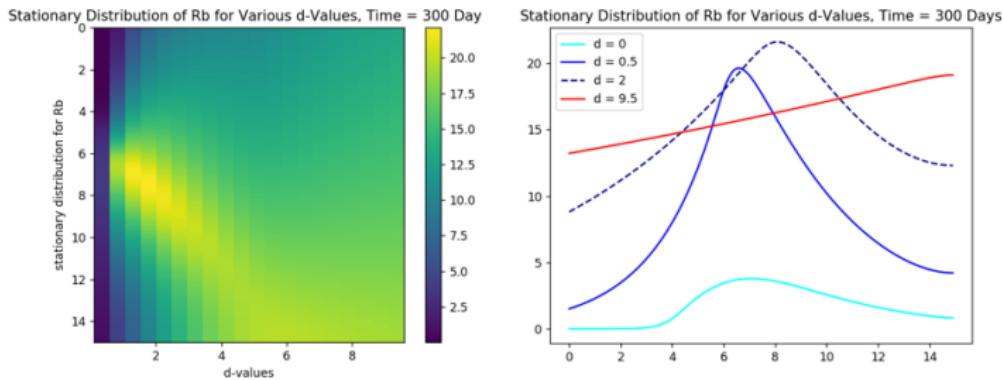
Looking at a lake with a set depth of 15m and changing d highlights how different turbulences affect the populations distribution.



- The distributions of A and R_b show striking peaks when d lies between 2m and 4m

Changing Turbulence for Lake of Depth 15m

A similar plot of bound nutrients show R_b actually peaks below A in the water

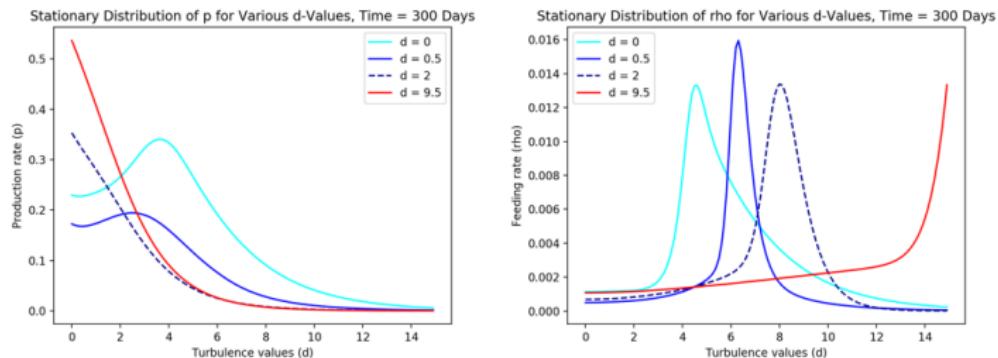


Possible explanations for this:

- High populations near surface create greater competition for nutrients and more light shading
- Sinking phytoplankton drag nutrients down with them
- These are released into the water when plankton die/sediment

Changing Turbulence

Plots of p and ρ show how growth rates and nutrient uptake settle into opposing gradients in high turbulence,



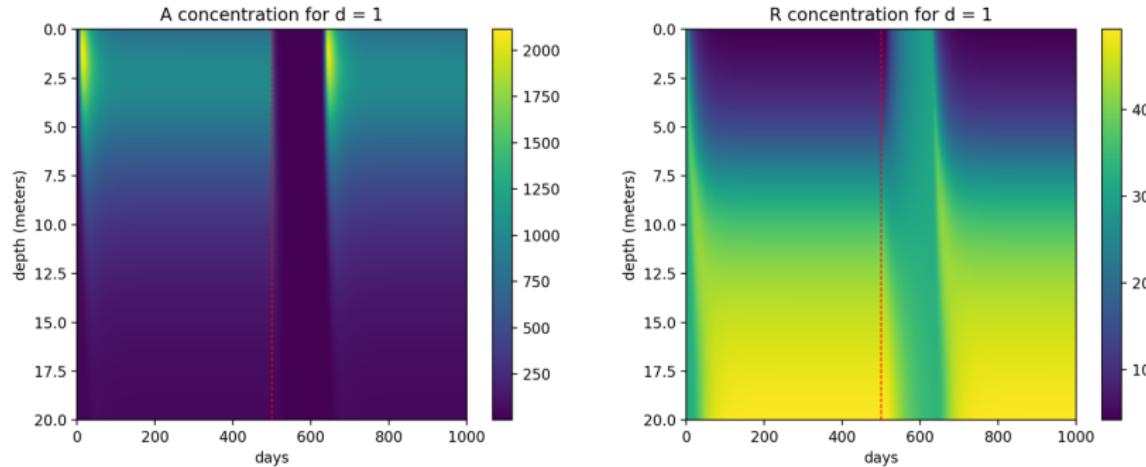
Growth is highest where there is most light and nutrient uptake is highest where the most nutrients are available.

Light Stress

- How do populations recover from extended periods of darkness, i.e. if an oil spill blocks all sunlight on the surface
- Do populations go extinct or are they resilient?
- By what mechanism do populations go extinct/survive?

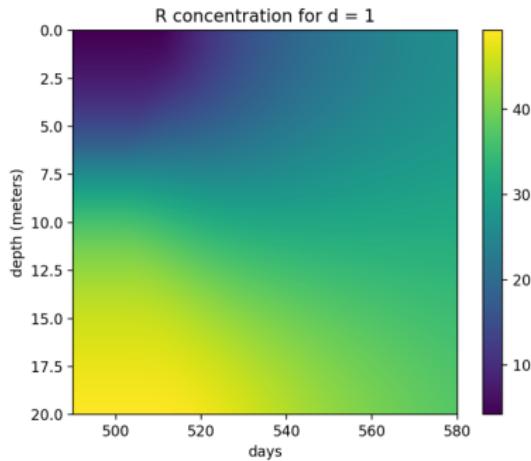
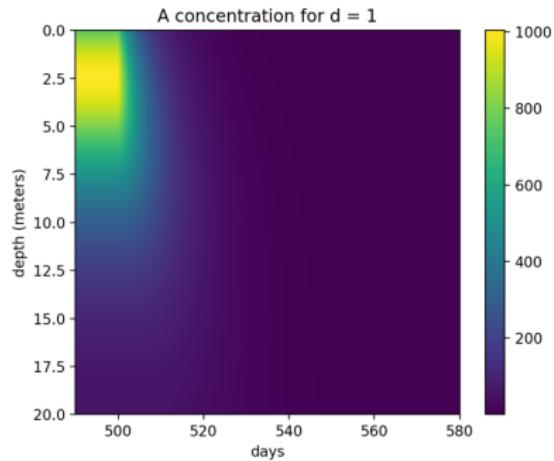
Changing Light

A 1000 day simulation shows populations recovering fully from light stresses and indicates that the system in this model is quite stable.



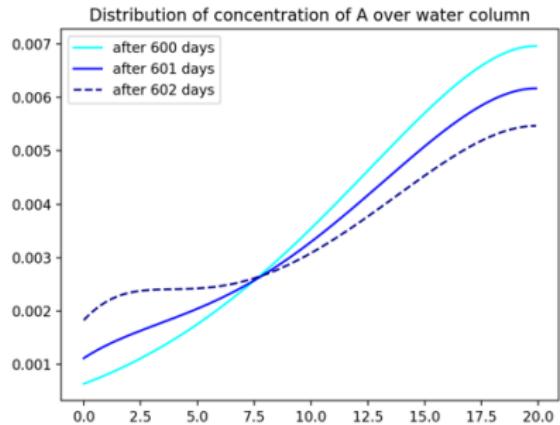
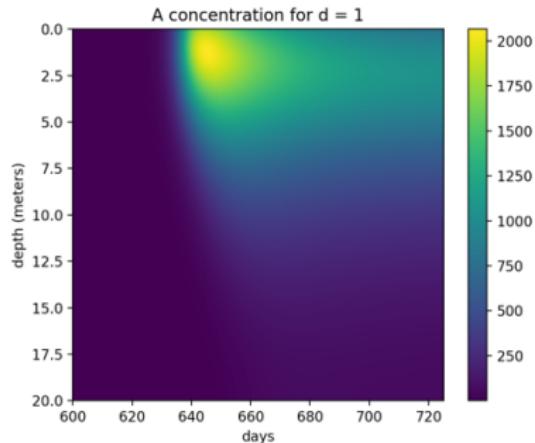
Light disappears for 100 days on the 500th day, marked with a red dashed line.

Changing Light (Zoomed-in)



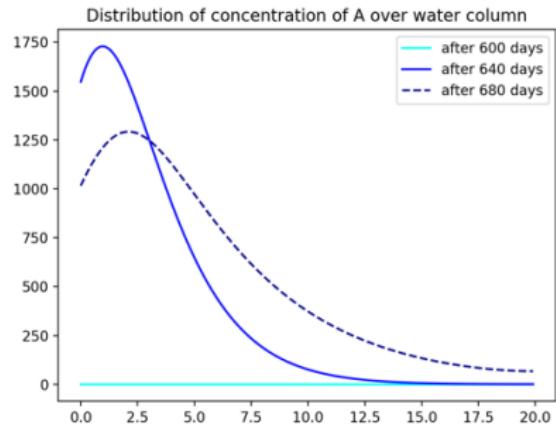
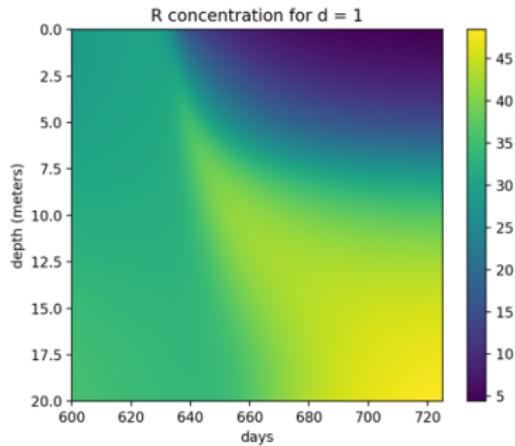
Enlargement of the day when light disappears: A 's population declines rapidly and R 's concentration settles gradually into a homogeneous distribution.

Changing Light (Zoomed-in)



Enlargement of the days when light returns to normal: Algal populations start increasing near the surface immediately and the distribution starts to homogenise. A "bump" starts to appear near the surface on the second day.

Changing Light (Zoomed-in)



The concentration of R become depleted at the surface within 60 days. Over the next 80 days there is a spike in A's population before it settles back to its stationary distribution.

Changing Light and Population Blooms

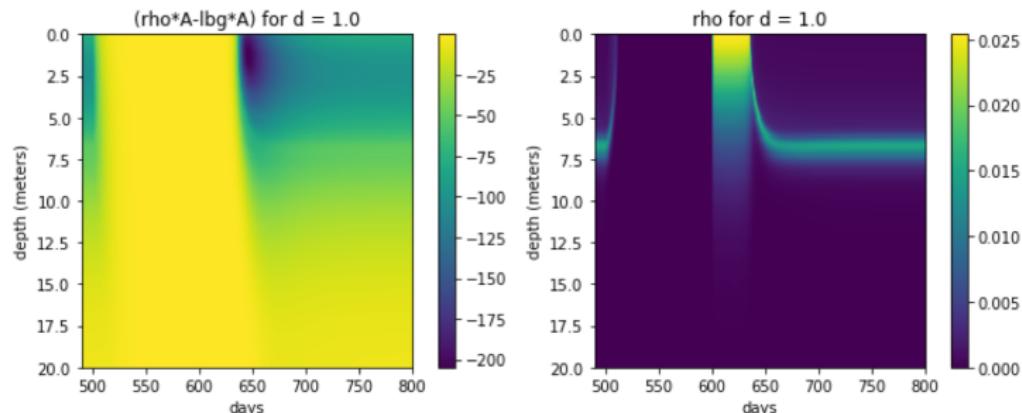
There are a number of contradicting hypothesis as to why phytoplankton population blooms occur in the ocean:

- The leading thought being that it is to do with the depth of the ocean's mixed-layer with shallower depths leading to greater populations¹².
- The bloom seen here would be more in line with a newer, alternative hypothesis which proposes that stress directly causes phytoplankton blooms if growth rates are positive even while population concentration is declining¹³

¹²Schverdrup's Critical Depth Hypothesis; 1953.

¹³Behrenfeld's Disturbance Recovery Hypothesis; 2010.

Changing Light and Growth Rates



- In this model ρA is the algal growth rate and $I_{bg} A$ is the loss rate
- $\rho A - I_{bg} A$ peaks below zero while there is no light and maintains these heightened value for 50 days after conditions return to normal
- the ρ function reaches it's maximum value at the surface during the 50 days after light returns

Changing Light

- These figures suggest that the negative disturbance to the light intensity has a short-term positive effect on the growth rate of the phytoplankton in this model
- This aligns better with the Alternative Disturbance Recovery Hypothesis than with the Critical Depth Hypothesis

Summary

What this project achieved:

- A finite difference approximation of the model¹⁴ was built which can be used to explore the influences of various factors on phytoplankton populations
- A number of interesting phenomena arose from this just this simple model (*e.g. population blooms after light stress, nontrivial peaks in distributions for certain turbulence values*)
- It is likely that further exploration of the model would yield more insights

¹⁴proposed by Jaeger et al. (2010).

Future Work

- Models like these are just a drop in the ocean compared to the true complexity of marine ecosystems and there are unlimited opportunities to improve them,
- further study of this model could search for tipping points caused by d or z_{max}
- the addition of more variables like predatory zooplankton
- introducing seasonality in the light intensity
- extending the model the 2-dimensions

Bibliography

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