Workshop: Resource competition and the paradox of the plankton

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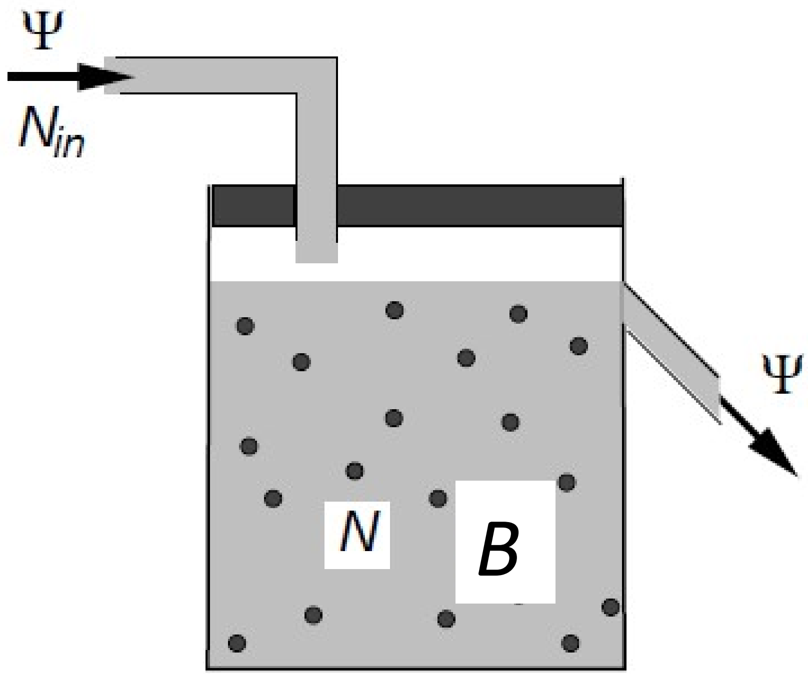
UH CMORE summer school

Motivation

- What sustains the diversity of phytoplankton?
  - G.E. Hutchinson, The Paradox of the Plankton, *Am. Nat.*, **95**, 137-145 (1961)
- Can we build simple, conceptual models that can maintain and explain co-existence of many phenotypes?
- These exercises present a first introduction to numerical modeling. Scripts explore the possibility of co-existence of phytoplankton types using concepts from resource competition theory.
- For more detailed perspectives on resource competition theory see D. Tilman *Resource competition and community structure*, Princeton (1982)

Basic concepts: Chemostat



- Ψ = l day^{-1}
- B = µmol l^{-1}
- N = µmol l^{-1}
- N_{in} = µmol l^{-1}
- V = l

Chemostat – nutrient and biomass

$$V\frac{dN}{dt} = -\mu VB + \Psi(N_{in} - N)$$

$$\Rightarrow \quad \frac{dN}{dt} = -\mu B + D(N_{in} - N)$$

$$\frac{dB}{dt} = \mu \frac{N}{N + k_N} B - DB$$

- B = μmol l^{-1}
- N = μmol l^{-1}
- N_{in} = μmol l^{-1}
- B_{in} = 0
- μ = d^{-1}
- D =Ψ/V d^{-1}

Resource limited growth – Monod kinetics

$$\frac{dN}{dt} = -\mu_o \frac{N}{N + k_N} B + D(N_{in} - N) \qquad (1)$$

$$\frac{dB}{dt} = \mu_o \frac{N}{N + k_N} B - DB \qquad (2)$$

- B = μmol l^{-1}
- N = μmol l^{-1}
- N_{in} = μmol l^{-1}
- μ_o = d^{-1}
- K_N = μmol l^{-1}
- D = Ψ/V d^{-1}
- Resource limited growth – Monod kinetics

Discretization and time-stepping

- Taylor Expansion

$$f(t+\Delta t) = f(t) + \Delta t\, f'(t) + O(\Delta t^2)$$

- So, neglecting $O(\Delta t^2)$ and higher order terms…

$$B(t+\Delta t) = B(t) + \frac{dB}{dt}\Delta t$$

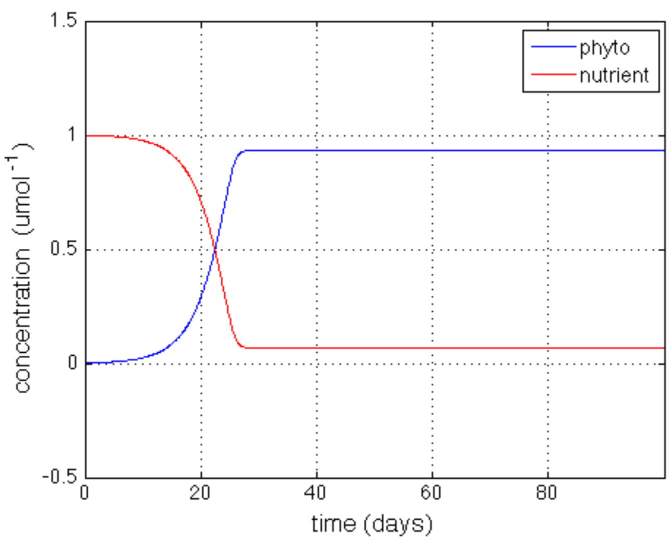
$$\frac{dB}{dt} = \mu \frac{N}{N+k_N} B - mB$$

- Evaluate dB/dt at time t, step forward with timestep Δt, repeat, …
- Euler forward step

Script 1: one_phyto_one_resource.m

Simple model of growth of the population of a single organism with single limiting resource

- *Run script – plots time dependent solution for resource and biomass*
  - Should look something like this:



Script 1: one_phyto_one_resource.m

- Numerical modeling issue - We must be careful about the timestep:
  - The default timestep in the script is 0.1 day ("deltat = 0.1;")
  - Try making the timestep 10 times smaller, and 10 times bigger.
    - In the script, change the value, save (click on disc image) and run (click on green arrow)
  - Does the solution change in either or both cases?
  - If so, what might be the reason?

Script 1: `one_phyto_one_resource.m`

- **Check: When steady state is reached do biomass and resource concentration match equilibrium solution for (1) and (2) with the given values for the variables?**
  - *The equilibrium resource concentration is "R*" in Resource Competition framework.*
- Modify parameters (half-saturation, max growth rate), run again. Can you make sense of the changes in solution by thinking about R*?

Script 2:
two_phyto_one_resource.m

- Added 2nd organism, still only one resource

$$\frac{dN}{dt} = -\mu_{o,1}\frac{N}{N+k_{N,1}}B_1 - \mu_{o,2}\frac{N}{N+k_{N,2}}B_2 + D(N_{in} - N) \quad (3)$$

$$\frac{dB_1}{dt} = \mu_{o,1}\frac{N}{N+k_{N,1}}B_1 - DB_1 \quad (4)$$

$$\frac{dB_2}{dt} = \mu_{o,2}\frac{N}{N+k_{N,2}}B_2 - DB_2 \quad (5)$$

Script 2: two_phyto_one_resource.m

- *Run script: Do both organisms survive at equilibrium?*
- *Find equilibrium solutions for (4) and (5).*
  - *Evaluate "subsistence concentration", R*(N), for each phytoplankton with its given parameters.*
  - *Does the lowest R* competitor always win?*

Script 2:
two_phyto_one_resource.m

- Try changing parameters to make higher R*(N) lower than competitor.
  - What happens to solution?
- *What happens if you set parameter values so R*(N) is equal (but growth rates are not the same) for both organisms?*
  - *See Hansen and Hubbell,* Science*, 207, 1491-1493 (1980) for laboratory demonstration.*

Script 2: two_phyto_one_resource.m

- **TIME VARYING RESOURCE SUPPLY**
- **Change the script so that the incoming nutrient concentration, N_{in} , varies in time; e.g.**

$$N_{in} = N_o(1 + 0.5\sin(\omega t))$$

- *you can uncomment line 55 in the script to make this happen, or you could try to add a line to the program yourself*

  - **What happens now?**
  - **Given that the ocean is always perturbed, is the solution from a perfectly steady resource supply plausible?**

Script 2:
two_phyto_one_resource.m

- **Time-dependent resource supply**
- **Change the script so that the incoming nutrient concentration, N_{in} , varies in time; e.g.**

$$N_{in} = N_o(1 + 0.5\sin(\omega t))$$

- *you can uncomment line 55 in the script to make this happen, or you could try to add a line to the program yourself*

  - **What happens now?**
  - **Given that the ocean is always perturbed, is the solution from a perfectly steady resource supply plausible?**

Script 2: two_phyto_one_resource.m

- **Non-linear mortality**
- We can add a mortality that depends on the square of the population density
  - Can you think why this might be a plausible form?

$$\frac{dB_1}{dt} = \mu_{o,1} \frac{N}{N + k_{N,1}} B_1 - DB_1 - mB_1^2 \qquad (4a)$$

$$\frac{dB_2}{dt} = \mu_{o,2} \frac{N}{N + k_{N,2}} B_2 - DB_2 - mB_2^2 \qquad (5a)$$

Script 2:
two_phyto_one_resource.m

- **Non-linear mortality**
- Using constant resource input, what happens if you add a quadratic loss term to the phytoplankton?
  - Modify the code…
    - You can simply uncomment lines 64 and 71 if you are not sure what to do. This will introduce a quadratic mortaility
  - What happens when you run the model now?

A little more advanced…

- Script three deals with two resources and two organisms.
- You can explore it to help get a feeling for Tilman's Resource Ratio Theory
  – The principle behind the lecture on understanding diazotroph biogeography

Script 3: two_phyto_two_resource.m

- Two resources N and P
- See Tilman, *Ecology,* **58**, 338-348, (1977)
- phytoplankton 1 and 2 have different P:N ratios (moles P: mole N); $R_{PN,1}$ and $R_{PN,2}$
- Liebig's Law of the minimum determines growth rate according to most limiting resource (for i=1,2)

$$\mu_i = \mu_{o,i} \min\left[\frac{N}{N + k_{N,i}}, \frac{P}{P + k_{P,i}}\right]$$

Script 3:
two_phyto_two_resource.m

- Constant N_{in}, P_{in}
- No additional mortality (dilution only, D)

1. *Make sure that one organism has lower R*(N) and the other lower R*(P)*
2. *Do you expect that both types can co-exist at equilibrium?*
3. *Test whether co-existence occurs for different ratios of P_{in}:N_{in}*
    1. *Experiment by changing values or automate search through parameter space using a for loop*

Script 3:
two_phyto_two_resource.m

1. *Write out the equations for nutrients and biomass (two nutrients, two biomass) when one organism is N limited, the other P limited*
2. *Assume equilibrium (d/dt = 0)*
3. *Solve the system of equations to determine range of* $P_{in}:N_{in}$ *over which co-existence should occur.*
    1. *HINT: Make simplifying assumption that* $N_{in} >> R^*(N)$ *and* $P_{in} >> R^*(P)$
4. *Do integrations of the script support you predictions?*