

Modelling Aquatic Ecosystems

Course 701-0426-00

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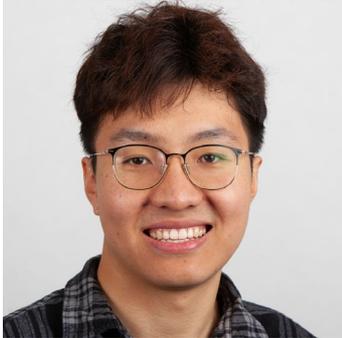


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Mechanistic Modelling of Aquatic Mesocosms



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PhD in Theoretical Physics
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Adjunct Professor at ETHZ

Retired since 2022



The students (you!) are able to

- **build** mathematical **models** of aquatic ecosystems that consider the most important biological, biogeochemical, and physical **processes**;
- **explain** the **interactions** between these processes and the **behavior** of the **system** that results from these interacting processes;
- **implement** and **apply** these ecological models;
- learn the key concepts of **model calibration** and the consideration of **stochasticity** and **uncertainty**.

Emphasis is on **integrating knowledge** in the form of models, on their use for **improving** the **understanding** and **management** of aquatic ecosystems and on their **limitations**.

- **Hands-on experience** with model **implementation, simulation, sensitivity analysis**, and discussion of the behavior of a series of ecosystem models of increasing complexity to deepen and extend the knowledge gained in the lectures
- Gain some **experience with R** (also useful for statistical data analysis in future projects)

Emphasis is on **improving the understanding** of the behavior of the models and the aquatic ecosystems, not on programming.

Basic knowledge about structure and functioning of **aquatic ecosystems** as well as about **analysis, differential equations, linear algebra** and **probability**.

The time for the exercises will be provided during the course.
This decreases the time for lectures and makes them quite intensive.
You will need time between the course hours to read the manuscript.

Approximate time budget (3 credit points = 75-90 hours study time):

25-30 hours: Course attendance including supervised exercise time

25-30 hours: Reading the manuscript and preparing exercises

25-30 hours: Preparation of your own model and the oral exam.

Course and exercises will take place Wednesday 10:15 - 12:00 in LFW B2

Please **install before the exercise**:

A current version of R (<http://www.r-project.org>),

the editor R-Studio (<http://www.rstudio.org>),

and the R-package ecosim: `install.packages(c("ecosim"))`

Introduction to R programming:

<https://cran.r-project.org/doc/contrib/Torfs+Brauer-Short-R-Intro.pdf>

Program, manuscript, exercises etc. can be downloaded from:

<http://www.eawag.ch/forschung/siam/lehre/modaqecosys>

There will be an **oral exam in the two weeks** after the semester **02.-13.06.25**

During the semester you will develop and implement your own model (in groups of two), interpret simulation results and perform a sensitivity analysis.

We will assign topics on 02.04.25.

Deadline for initial code submission: 08.05.25

Deadline for submission of R-files, results and interpretation: 23.05.25

This is mandatory for being admitted to the exam! In the oral exam we will start with questions about your model before moving on to other topics.

Use the time in the exercises to ask questions and get help!
Don't do it last minute.

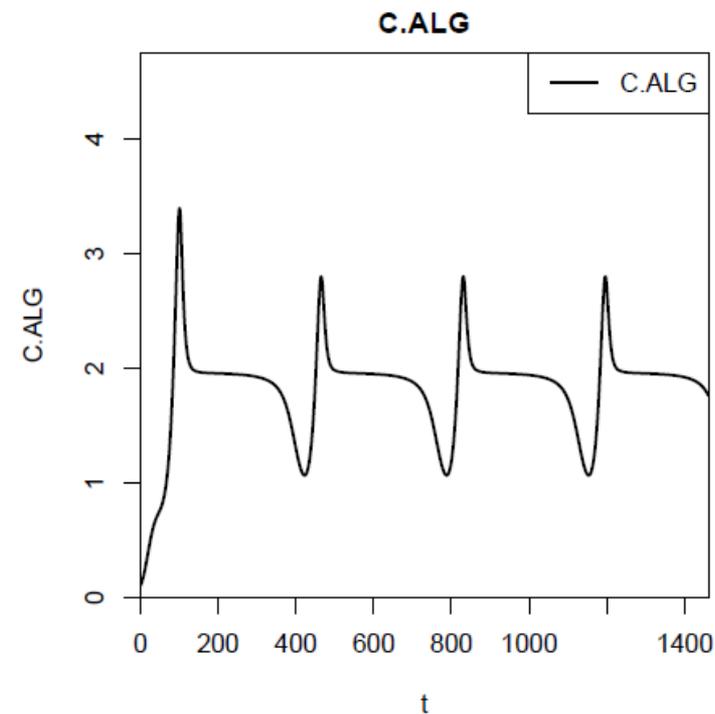
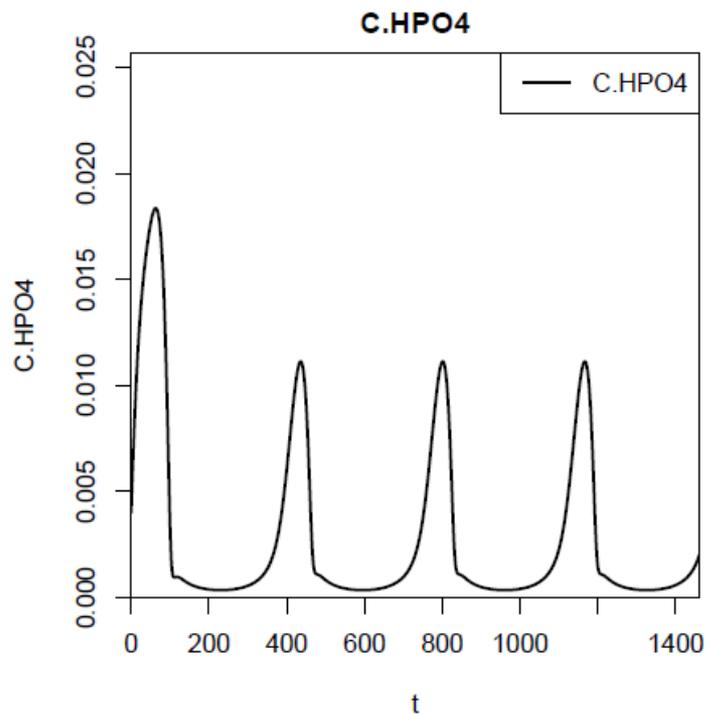
- 1 Introduction
- I Basic Concepts**
 - 2 Principles of Modelling Environmental Systems
 - 3 Formulation of Mass Balance Equations
 - 4 Formulation of Transformation Processes
 - 5 Behaviour of Solutions of ODE models
- II Formulation of Ecosystem Processes**
 - 6 Physical Processes
 - 7 Chemical Processes
 - 8 Biological Processes
- III Stochasticity, Uncertainty and Parameter Estimation**
 - 9 Consideration of Stochasticity and Uncertainty
 - 10 Parameter Estimation
- IV Simple Models of Aquatic Ecosystems**
 - 11 Simple Models of Aquatic Ecosystems
- V Advanced Aquatic Ecosystem Modelling**
 - 12 Extensions of Processes and Model Structure
 - 13 Research Models of Aquatic Ecosystems

1. Introduction, principles of modelling environmental systems, mass balance in a mixed reactor, process table notation, simple lake plankton model
Exercise: R, ecosim-package, simple lake plankton model
Exercise: lake phytoplankton-zooplankton model
2. Process stoichiometry Exercises: analytical solution, calculation with stoichcalc
3. Biological processes in lakes
4. Physical processes in lakes, mass balance in multi-box and continuous systems Exercise: structured, biogeochemical-ecological lake model
Assignments: build your own model by implementing model extensions
5. Physical processes in rivers, bacterial growth, river model for benthic populations Exercise: river model for benthic populations, nutrients and oxygen
6. Uncertainty, Parameter estimation, Stochasticity
Exercise: parameter estimation
Exercise: stochasticity, uncertainty
7. Existing models and applications in research and practice, examples and case studies, preparation of the oral exam, feedback



Questions?

- Acquire basic knowledge of the formulation of transport and transformation processes to formulate a simple lake plankton model.
- Become familiar with the process table notation and rate formulation that will be the basis of the more complex models.



What's your motivation to learn ecosystem modelling?

chapter 1

- 1. Improving understanding of ecosystem function:**
Test of quantitatively formulated hypotheses about system mechanisms. Estimation of fluxes and conversion rates.
Stimulation of thinking about the function of an ecosystem.
- 2. Summarizing and communicating knowledge:**
Ecosystem models are perfect communication tools for exchanging quantitatively formulated knowledge of the processes in the ecosystem. A systematic notation facilitates the use of models for this purpose significantly.
- 3. Supporting ecosystem management:**
Prediction of the consequences of suggested measures.
Estimation and consideration of prediction uncertainty is essential for this purpose of ecosystem modelling.

Pelagic zone:

Water body not close to sediment and shore or bank.

Litoral zone:

Water body close to the shore or bank and the adjacent periodically inundated area.

Benthic zone:

Water body above the sediment and the top sediment layers.

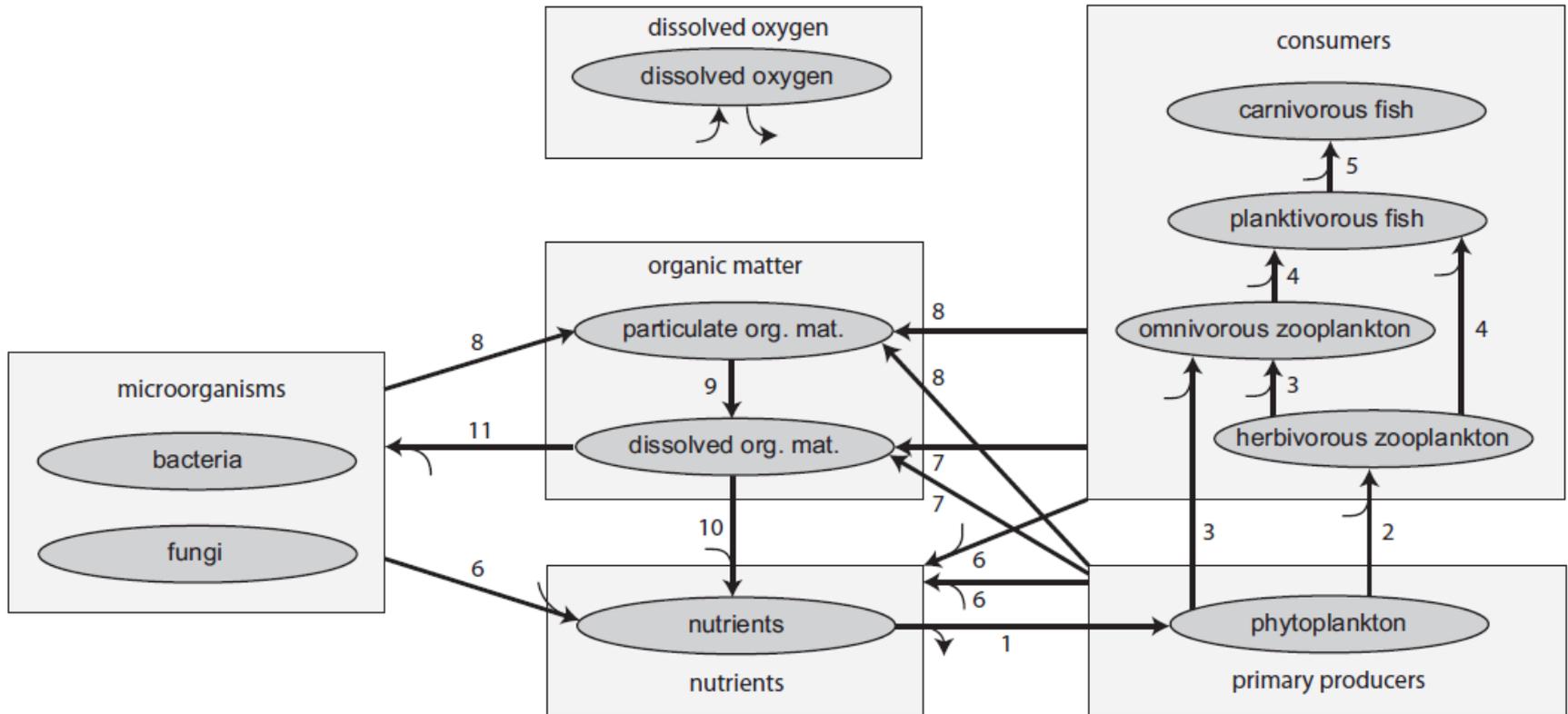
Interstitial zone:

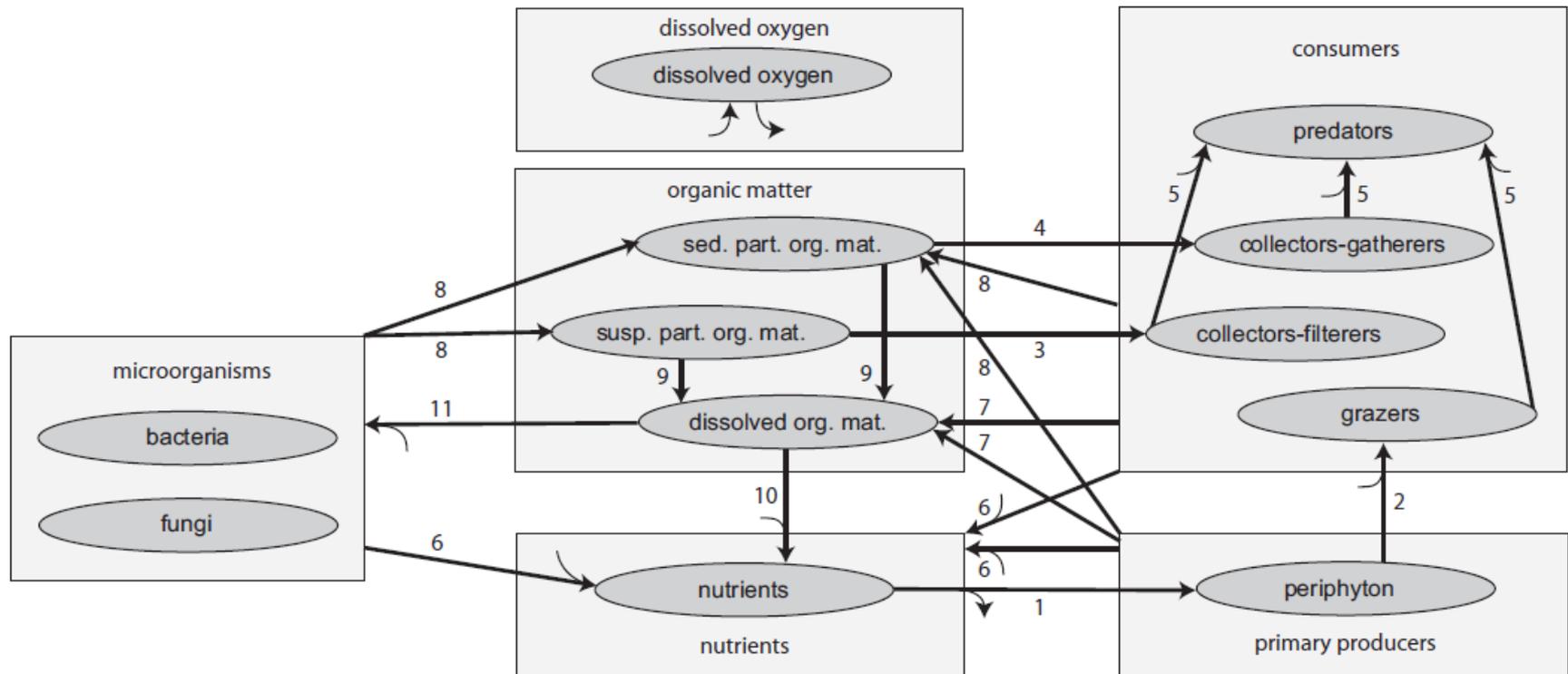
Pore space in the sediment below the benthic zone.

Imagine your favorite lake or stream...

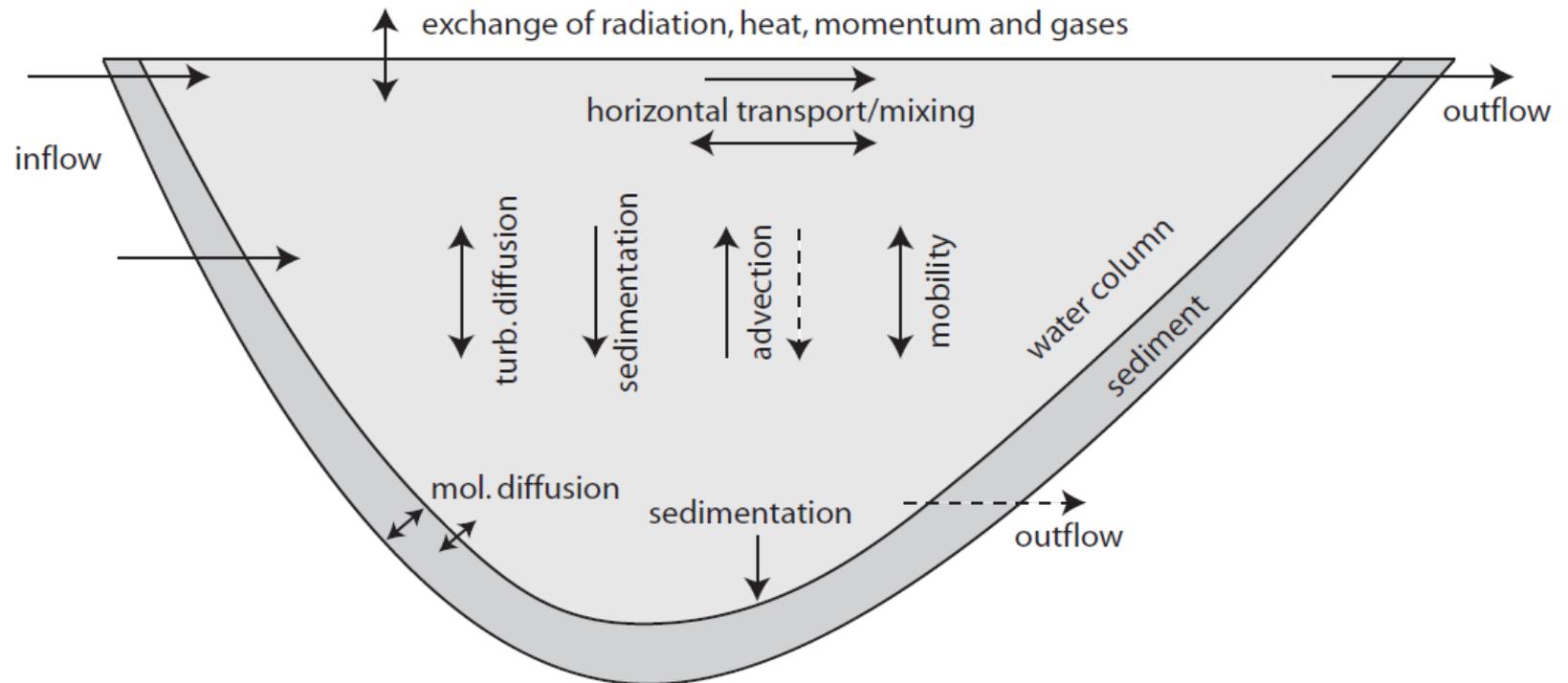


To draw the food-web of this system, what are important organism groups to consider and what do they feed on?

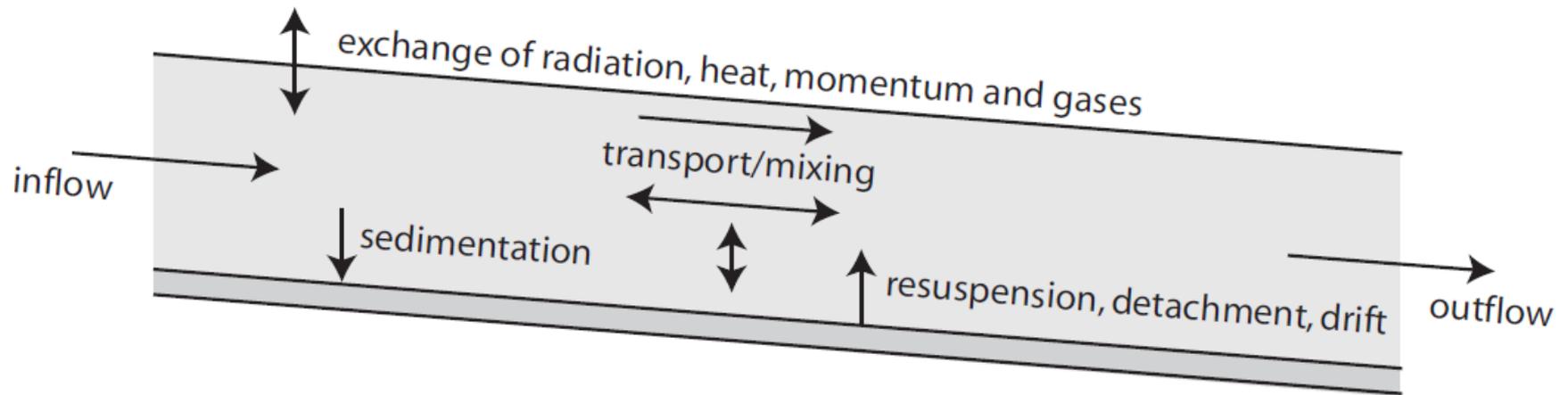


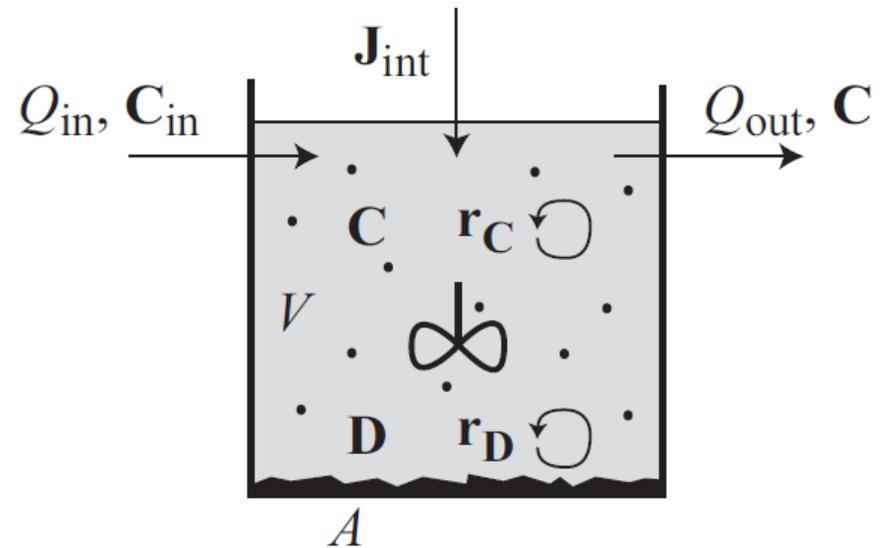


Transport Processes in a Lake

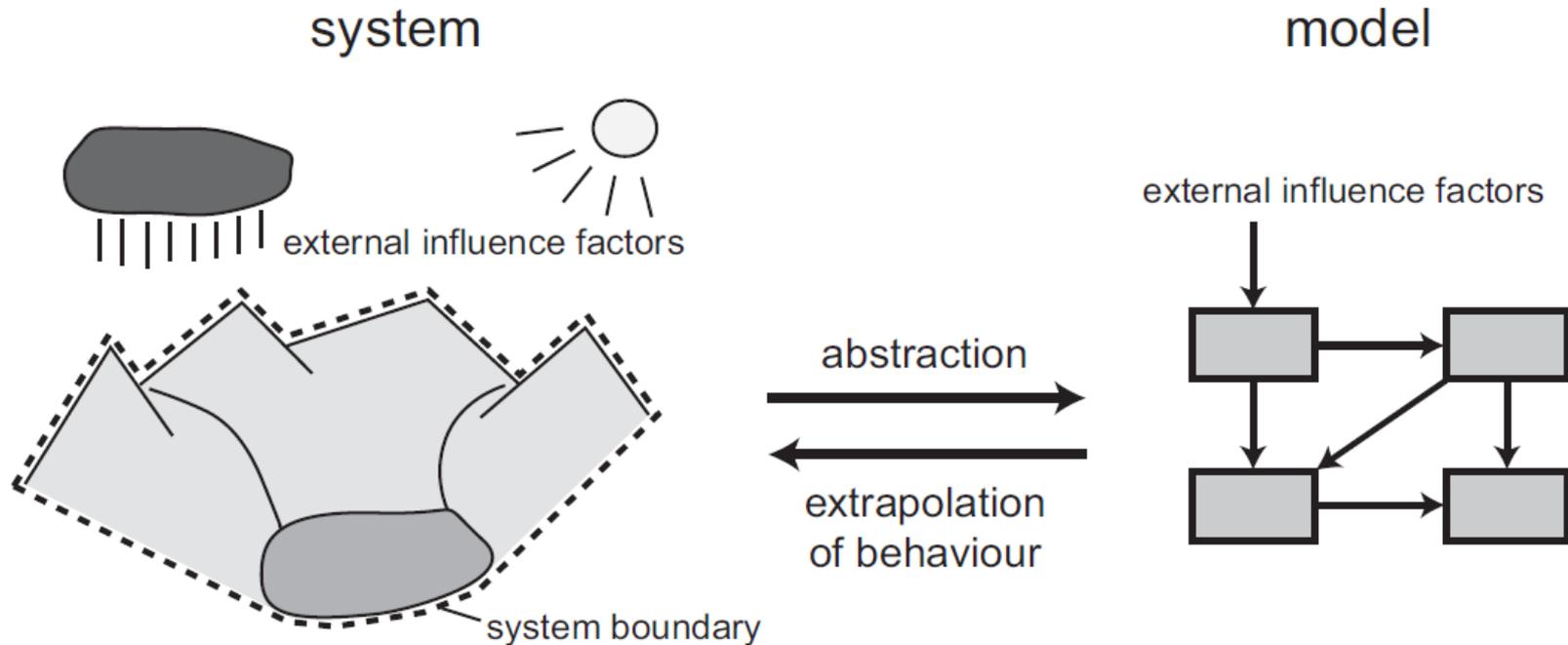


Transport Processes in a River





Meaning of models



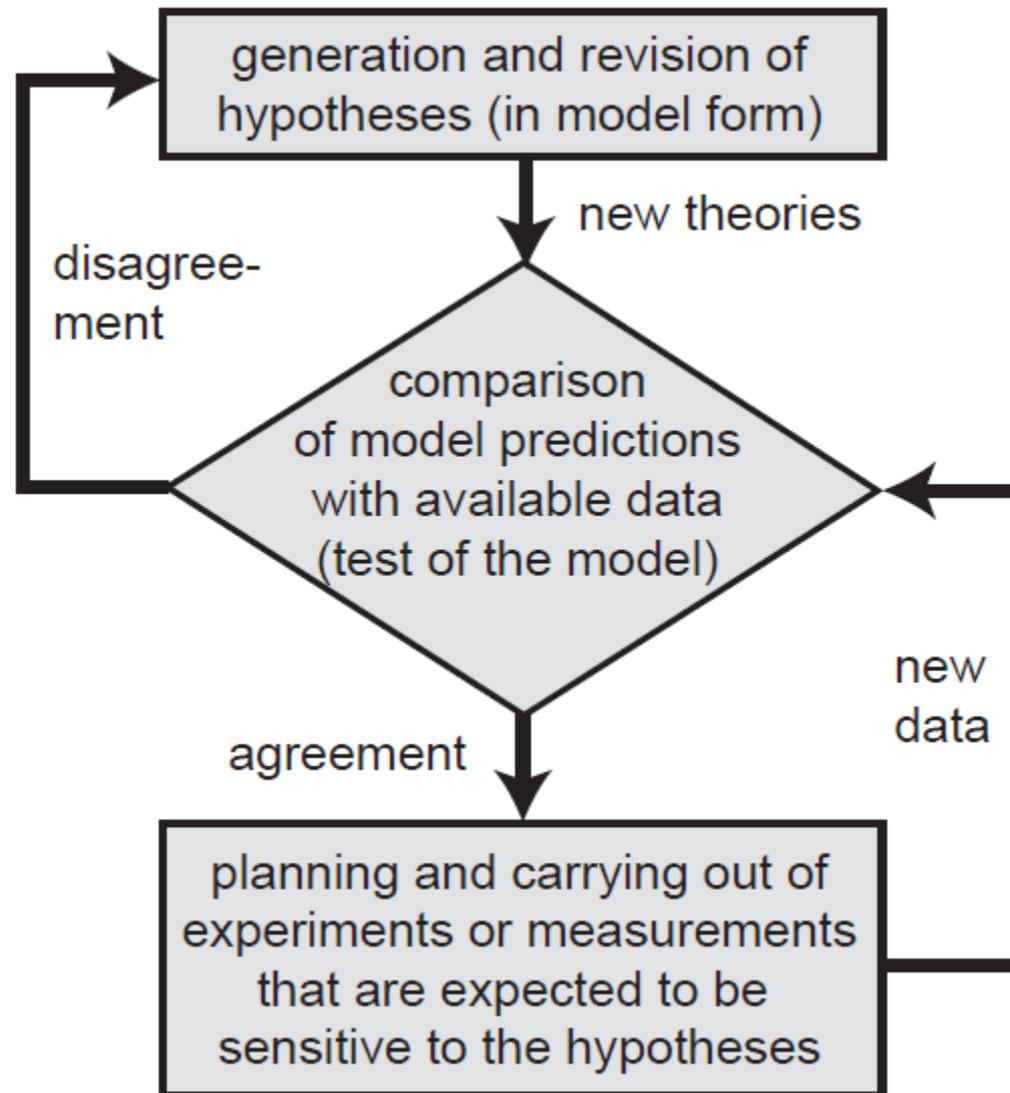
- many (rather arbitrary) choices and assumptions!
- model has to fit the purpose!

Formulation of ecosystem models

Essential techniques: Empirical relationships and mass-balance equations.

Typical form of an environmental model:

Mechanistic description of mass conservation - use of empirical expressions for the formulation of transformation and transfer processes.



Mathematical Model: Simplified mathematical description of a (real) system

$$y = ax + b$$

$$dy/dt = a*x(t)*y - b*y$$

Input variable: External influence factor, predictor / explanatory / independent variable

x

Output variable: State / response / dependent variable

y

Parameter: (Unknown) variable needed to relate input to output a, b

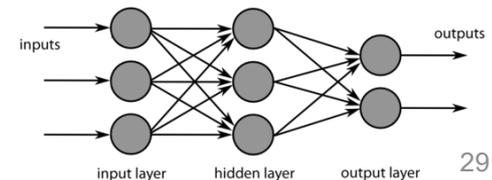
Mechanistic models (aka process-based, causal models)

- are *knowledge/theory* driven, *explicitly* describe mechanisms/processes to relate input and output
- parameters have a (physical, biological) meaning, **are not necessarily calibrated**

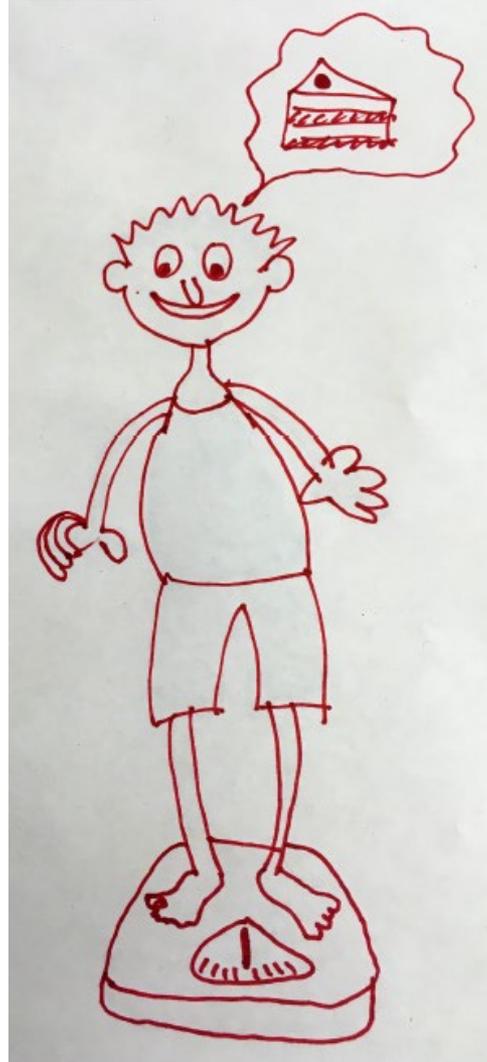
e.g.: individual based models, population / predator-prey / food web / community models based on ordinary differential equations, meta-community models, ecosystem models

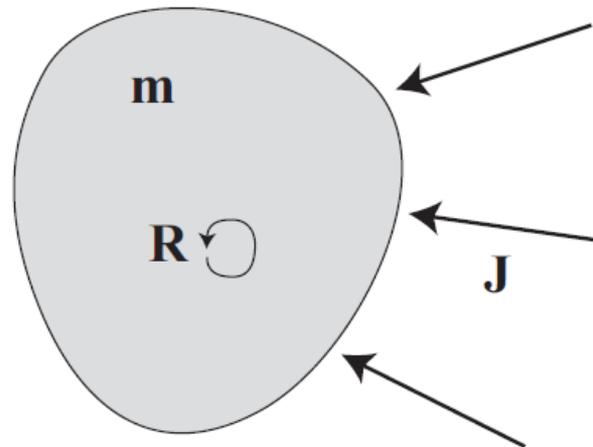
Empirical models

- are *data* driven, based on empirical relationship between input and output
- a) **Statistical models:** **parameters are calibrated**, do not have a (physical, biological) meaning, still interpretable, make statistical assumptions that can be tested
e.g. multivariate regression models, autoregressive time series models
- b) **Machine learning algorithms:** parameters are (usually) not interpretable, do not make statistical assumptions, are typically perceived as "black box"
e.g. (deep) artificial neural networks, random forests, boosted regression



chapter 3.1





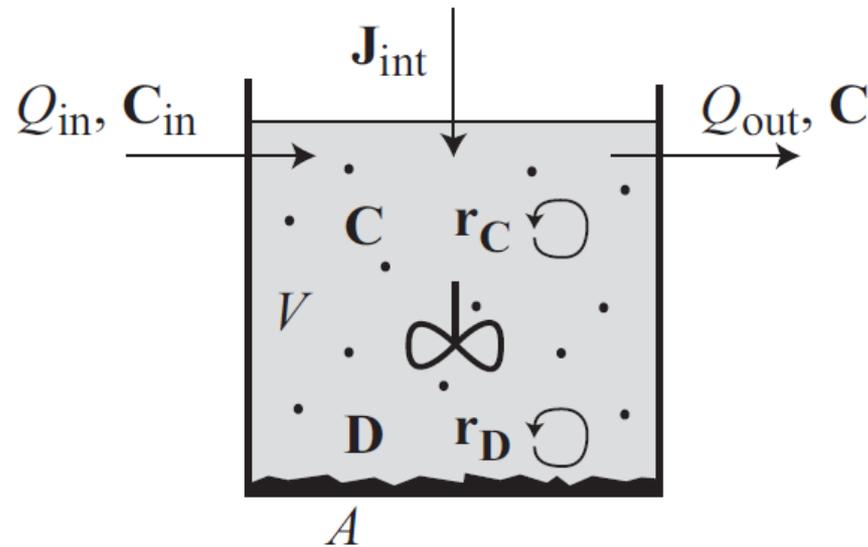
m "masses" [m], **J** (net) inputs [m/T], **R** (net) production [m/T]

Integral form: calculate "mass" at t_{end} from "mass" at t_{ini} by adding net inputs and net production:

$$\mathbf{m}(t_{\text{end}}) = \mathbf{m}(t_{\text{ini}}) + \int_{t_{\text{ini}}}^{t_{\text{end}}} \mathbf{J}(t) dt + \int_{t_{\text{ini}}}^{t_{\text{end}}} \mathbf{R}(t) dt$$

Differential form: substitute t_{end} with t and differentiate:

$$\frac{d\mathbf{m}}{dt}(t) = \mathbf{J}(t) + \mathbf{R}(t)$$



C concentration [M/L^3]

D surface density [M/L^2]

Q_{in} inflow, Q_{out} outflow [L^3/T]

J_{int} flux across the interface [M/T]

$$\mathbf{m} = \begin{pmatrix} V \\ VC_1 \\ VC_2 \\ \vdots \\ VC_{n_v} \\ AD_1 \\ AD_2 \\ \vdots \\ AD_{n_a} \end{pmatrix}, \quad \mathbf{J} = \begin{pmatrix} Q_{in} - Q_{out} \\ Q_{in}C_{in,1} - Q_{out}C_1 + J_{int,1} \\ Q_{in}C_{in,2} - Q_{out}C_2 + J_{int,2} \\ \vdots \\ Q_{in}C_{in,n_s} - Q_{out}C_{n_s} + J_{int,n_v} \\ 0 \\ 0 \\ \vdots \\ 0 \end{pmatrix}, \quad \mathbf{R} = \begin{pmatrix} 0 \\ VrC_1 \\ VrC_2 \\ \vdots \\ VrC_{n_v} \\ Ar_{D_1} \\ Ar_{D_2} \\ \vdots \\ Ar_{D_{n_a}} \end{pmatrix}$$

\mathbf{m} "masses" [m], \mathbf{J} (net) inputs [m/T], \mathbf{R} (net) production [m/T]

$$\mathbf{C} = \begin{pmatrix} C_1 \\ C_2 \\ \vdots \\ C_{n_v} \end{pmatrix}, \quad \mathbf{J}_{\text{int}} = \begin{pmatrix} J_{\text{int},1} \\ J_{\text{int},2} \\ \vdots \\ J_{\text{int},n_v} \end{pmatrix}, \quad \mathbf{r}_C = \begin{pmatrix} r_{C_1} \\ r_{C_2} \\ \vdots \\ r_{C_{n_v}} \end{pmatrix}$$

$$\mathbf{D} = \begin{pmatrix} D_1 \\ D_2 \\ \vdots \\ D_{n_a} \end{pmatrix}, \quad \mathbf{r}_D = \begin{pmatrix} r_{D_1} \\ r_{D_2} \\ \vdots \\ r_{D_{n_a}} \end{pmatrix}$$

$$\frac{dV}{dt} = Q_{\text{in}} - Q_{\text{out}}$$

$$\frac{d}{dt}(V\mathbf{C}) = Q_{\text{in}}\mathbf{C}_{\text{in}} - Q_{\text{out}}\mathbf{C} + \mathbf{J}_{\text{int}} + V\mathbf{r}_{\mathbf{C}}$$

$$\frac{d}{dt}(A\mathbf{D}) = A\mathbf{r}_{\mathbf{D}}$$

$$\frac{dV}{dt} = Q_{\text{in}} - Q_{\text{out}}$$

$$\frac{d\mathbf{C}}{dt} = \frac{Q_{\text{in}}}{V} (\mathbf{C}_{\text{in}} - \mathbf{C}) + \frac{\mathbf{J}_{\text{int}}}{V} + \mathbf{r}_{\mathbf{C}}$$

$$\frac{d\mathbf{D}}{dt} = \mathbf{r}_{\mathbf{D}}$$

Differential Equations

Example 11.1

$$\frac{dC_{\text{HPO}_4}}{dt} = \overbrace{\frac{Q_{\text{in}}}{V} (C_{\text{HPO}_4, \text{in}} - C_{\text{HPO}_4})}^{\text{net input via in/outflow}} \underbrace{- \alpha_{\text{P,ALG}} \cdot k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}}}_{\text{consumption by algae}}$$

$$\frac{dC_{\text{ALG}}}{dt} = \overbrace{-\frac{Q_{\text{in}}}{V} C_{\text{ALG}}}^{\text{loss via outflow}} + \overbrace{k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}}}_{\text{growth of algae}} - \underbrace{k_{\text{death,ALG}} C_{\text{ALG}}}_{\text{death of algae}}$$

Process	Substances					Rate
	s_1	s_2	s_3	\dots	s_{n_s}	
p_1	ν_{11}	ν_{12}	ν_{13}	\dots	ν_{1n_s}	ρ_1
p_2	ν_{21}	ν_{22}	ν_{23}	\dots	ν_{2n_s}	ρ_2
\vdots	\vdots	\vdots	\vdots	\ddots	\vdots	\vdots
p_{n_p}	$\nu_{n_p 1}$	$\nu_{n_p 2}$	$\nu_{n_p 3}$	\dots	$\nu_{n_p n_s}$	ρ_{n_p}

Substance transformation rate in homogeneous environment:

$$r_j = \sum_{i=1}^{n_p} \nu_{ij} \rho_i$$

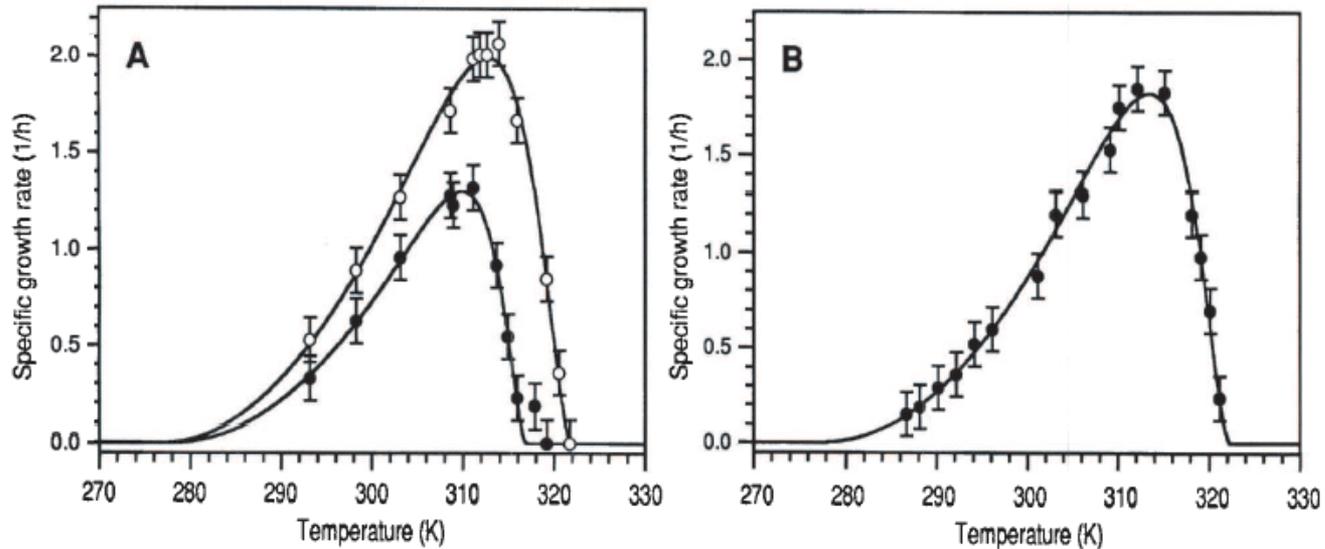
One of the (non-zero) stoichiometric coefficients, ν_{ij} , in each row can be selected to be plus or minus unity. This makes the corresponding process rate, ρ_j , to the (positive or negative) contribution of this process to the total transformation rate of the corresponding substance, s_i .

Process rate with maximum/standard specific growth rate and non-dimensional modification factors that account for the influence of temperature, light intensity, nutrients, etc.

$$\rho_{\text{gro,ALG}} = k_{\text{gro,ALG},T_0} \cdot f_{\text{temp}}(T) \cdot f_{\text{rad}}(I) \cdot f_{\text{lim}}(C_{\text{HPO}_4^{2-}}, C_{\text{NH}_4^+}, C_{\text{NO}_3^-}) \cdot C_{\text{ALG}}$$

$$\rho_{\text{miner,anox,POM}} = k_{\text{miner,anox,POM},T_0} \cdot f_{\text{temp}}(T) \cdot f_{\text{inh}}(C_{\text{O}_2}) \cdot f_{\text{lim}}(C_{\text{NO}_3^-}) \cdot C_{\text{POM}}$$

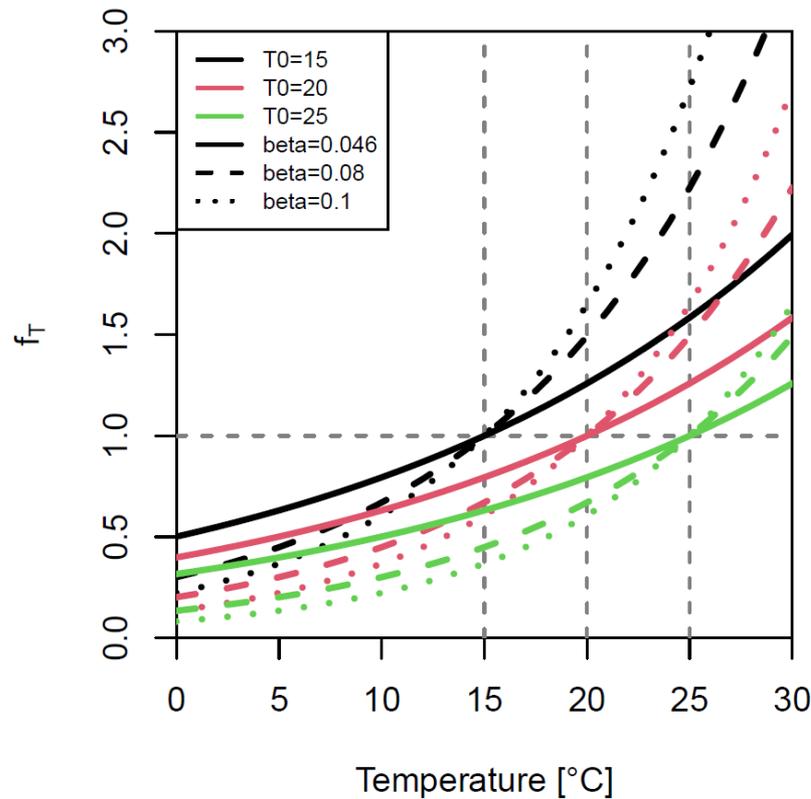
Temperature dependence factor



Exponential:

$$f_{\text{temp}}^{\text{exp}}(T) = \exp(\beta(T - T_0))$$

Temperature dependence factor



Exponential:

$$f_{\text{temp}}^{\text{exp}}(T) = \exp(\beta(T - T_0))$$

Limitation by substance concentrations

Monod:

$$f_{\text{lim}}^{\text{Monod}}(C) = \frac{C}{K + C}$$

Exponential:

$$f_{\text{lim}}^{\text{exp}}(C) = 1 - \exp\left(-\frac{C}{K}\right)$$

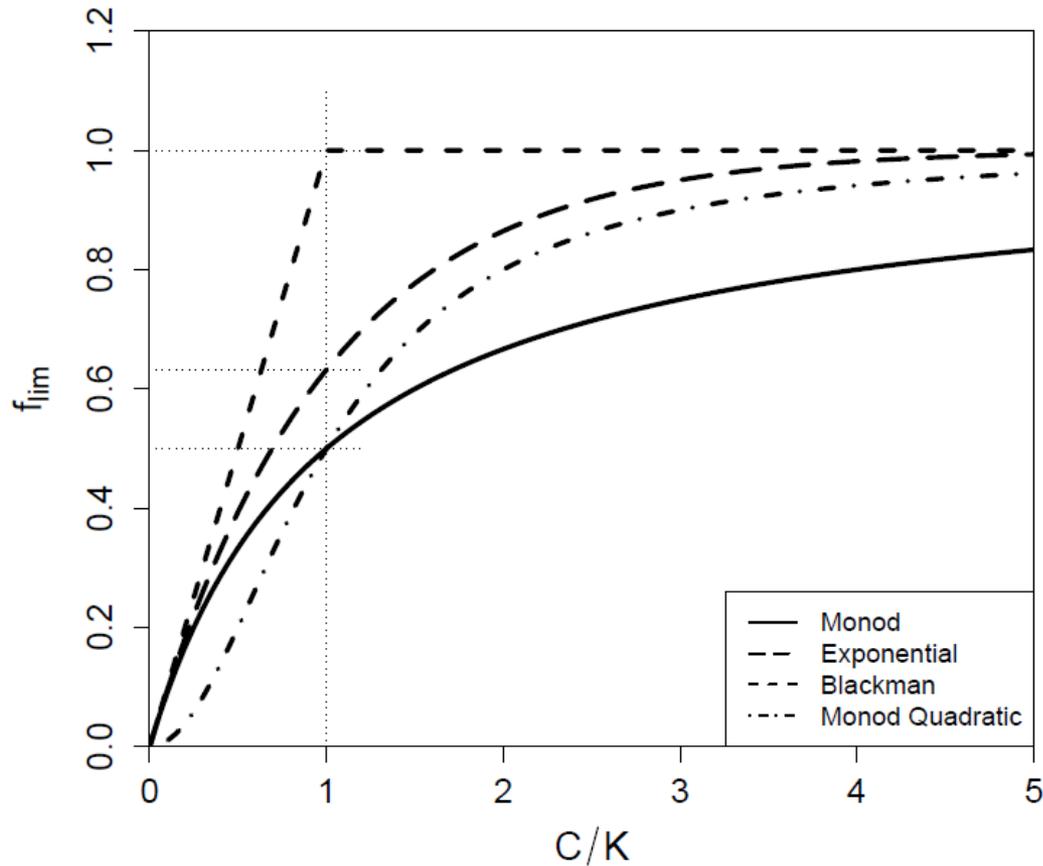
Blackman:

$$f_{\text{lim}}^{\text{Blackman}}(C) = \begin{cases} \frac{C}{K} & \text{for } C < K \\ 1 & \text{for } C \geq K \end{cases}$$

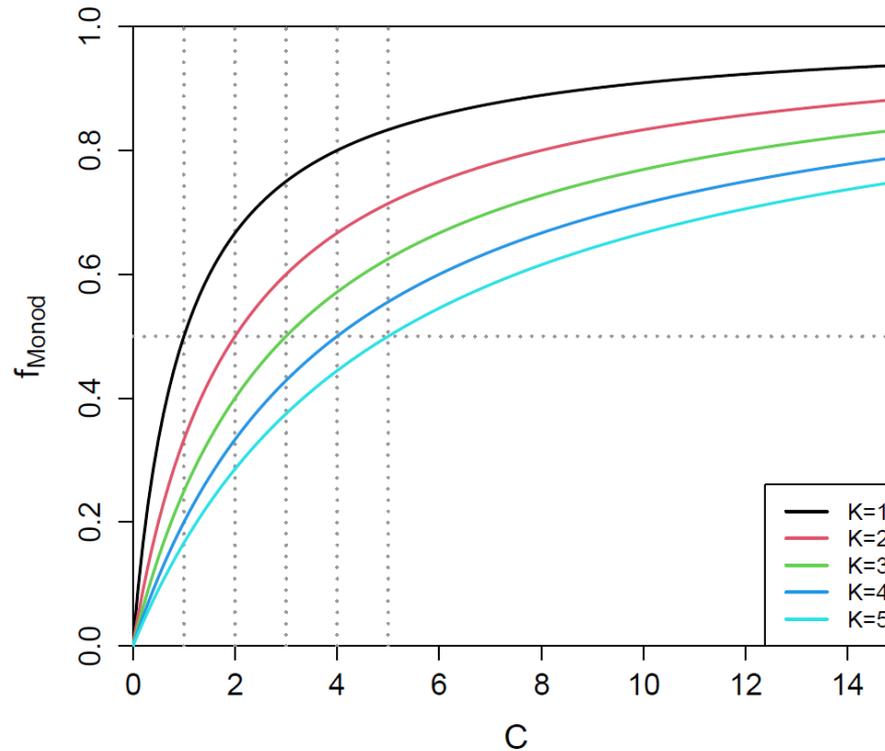
Monod Quadratic:

$$f_{\text{lim}}^{\text{Monodquad}}(C) = \frac{C^2}{K^2 + C^2}$$

Limitation by substance concentrations



Limitation by substance concentrations



$$f_{\text{lim}}^{\text{Monod}}(C) = \frac{C}{K + C}$$

Limitation by multiple substances

Product:

$$f_N(C_{\text{HPO}_4}, C_{\text{NH}_4}, C_{\text{NO}_3}) = \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} \cdot \frac{C_{\text{NH}_4} + C_{\text{NO}_3}}{K_N + C_{\text{NH}_4} + C_{\text{NO}_3}}$$

Minimum (Liebig's Law):

$$f_N(C_{\text{HPO}_4}, C_{\text{NH}_4}, C_{\text{NO}_3}) = \min \left(\frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}}, \frac{C_{\text{NH}_4} + C_{\text{NO}_3}}{K_N + C_{\text{NH}_4} + C_{\text{NO}_3}} \right)$$

Inhibition by substance concentrations

Monod:

$$f_{\text{inh}}^{\text{Monod}}(C) = \frac{K}{K + C}$$

Exponential:

$$f_{\text{inh}}^{\text{exp}}(C) = \exp\left(-\frac{C}{K}\right)$$

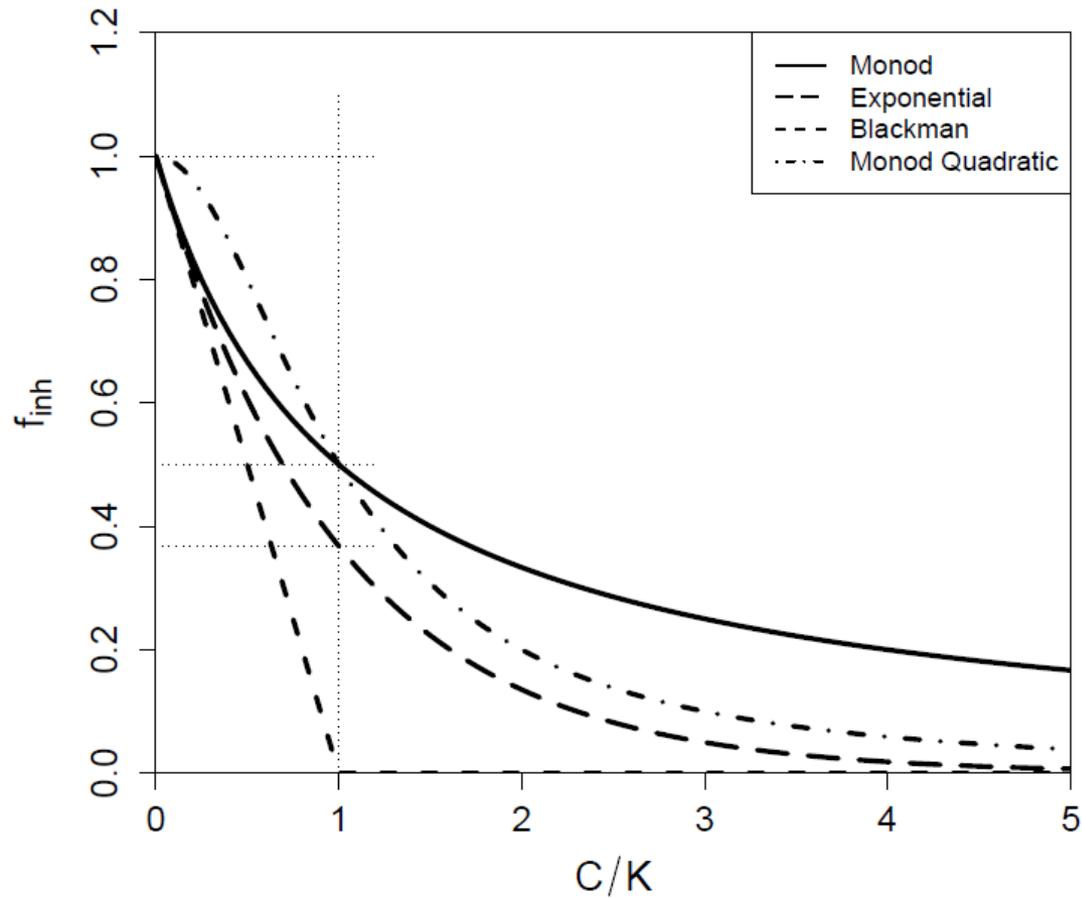
Blackman:

$$f_{\text{inh}}^{\text{Blackman}}(C) = \begin{cases} 1 - \frac{C}{K} & \text{for } C < K \\ 0 & \text{for } C \geq K \end{cases}$$

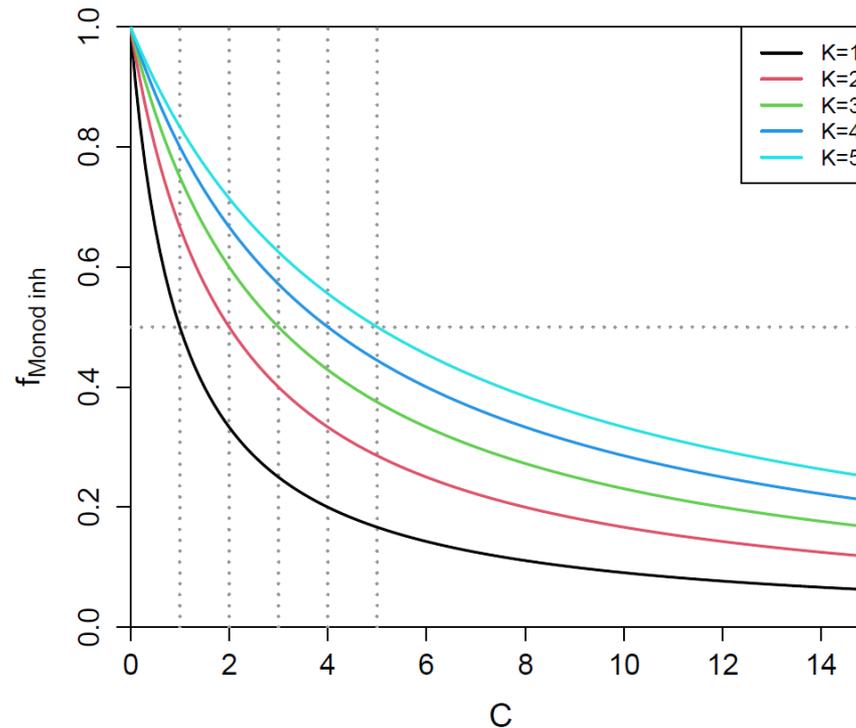
Monod Quadratic:

$$f_{\text{inh}}^{\text{Monodquad}}(C) = \frac{K^2}{K^2 + C^2}$$

Inhibition by substance concentrations



Inhibition by substance concentrations



$$f_{\text{inh}}^{\text{Monod}}(C) = \frac{K}{K + C}$$

Light dependence factor

Monod:

$$f_{\text{rad}}^{\text{Monod}}(I) = \frac{I}{K_I + I}$$

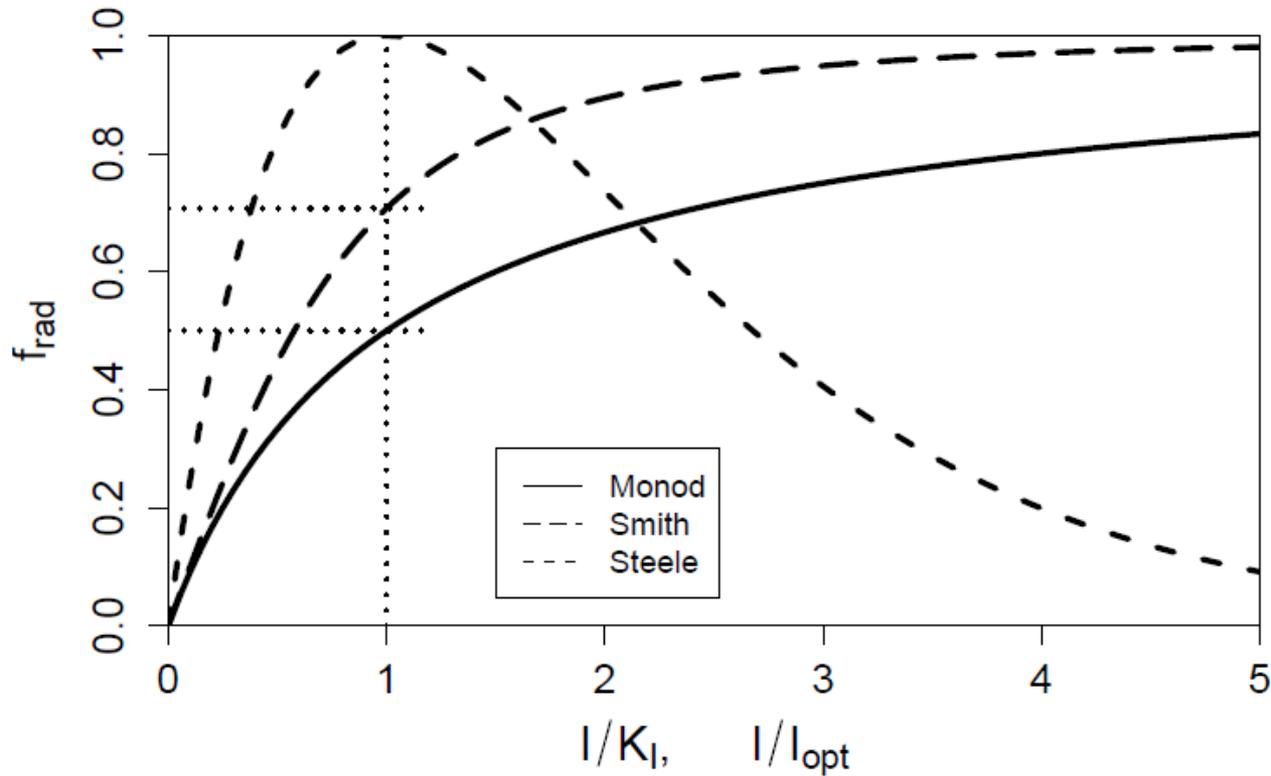
Smith:

$$f_{\text{rad}}^{\text{Smith}}(I) = \frac{I}{\sqrt{K_I^2 + I^2}}$$

Steele:

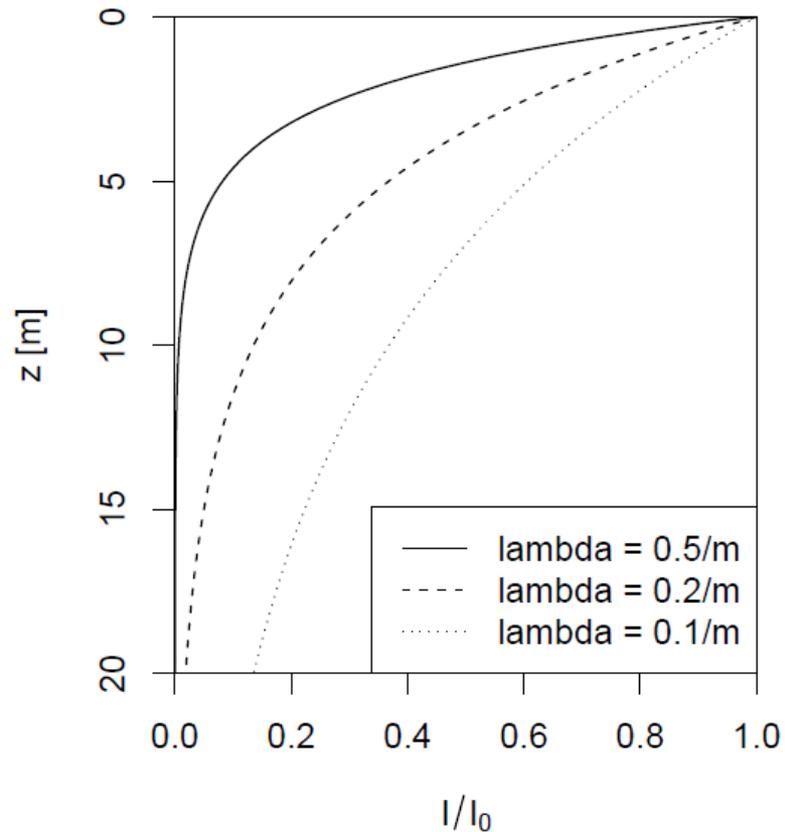
$$f_{\text{rad}}^{\text{Steele}}(I) = \frac{I}{I_{\text{opt}}} \exp\left(1 - \frac{I}{I_{\text{opt}}}\right)$$

Light dependence factors



Light attenuation:

$$I(z) = I_0 \exp(-\lambda z);$$



Light attenuation

For a model with a mixed reactor, the light dependence factor (and not the light itself!) has to be averaged across depth.

Average light dependence factor:

$$\bar{f}_{\text{rad}}(I_0, \lambda, h) = \frac{1}{h} \int_0^h f_{\text{rad}}(I_0 \exp(-\lambda z)) dz$$

Average light dependence factors

Monod:

$$\bar{f}_{\text{rad}}^{\text{Monod}}(I_0, \lambda, h) = \frac{1}{\lambda h} \log \left(\frac{K_I + I_0}{K_I + I_0 \exp(-\lambda h)} \right)$$

Smith:

$$\bar{f}_{\text{rad}}^{\text{Smith}}(I_0, \lambda, h) = \frac{1}{\lambda h} \log \left(\frac{\frac{I_0}{K_I} + \sqrt{1 + \left(\frac{I_0}{K_I}\right)^2}}{\frac{I_0 \exp(-\lambda h)}{K_I} + \sqrt{1 + \left(\frac{I_0 \exp(-\lambda h)}{K_I}\right)^2}} \right)$$

Steele:

$$\bar{f}_{\text{rad}}^{\text{Steele}}(I_0, \lambda, h) = \frac{e}{\lambda h} \left[\exp \left(-\frac{I_0 \exp(-\lambda h)}{I_{\text{opt}}} \right) - \exp \left(-\frac{I_0}{I_{\text{opt}}} \right) \right]$$

Preference Among Different Food Sources

Many organisms can grow on different food sources.

As the stoichiometry and kinetics of growth on one food source may be different from that on another, it is best to represent growth on different food sources by different processes.

The process rates of these processes can still have many terms in common. But they also need a preference factor that depends on the concentrations of all food sources.

Preference Among Different Food Sources

Simplest conceptually satisfying expression:

$$f_{\text{pref}}^i(C_1, \dots, C_n) = \frac{p_i C_i}{\sum_{j=1}^n p_j C_j}$$

n : food sources with concentrations C_1, \dots, C_n ,

p_j : preference coefficient for food source j .

Process Table

Process	Substances / Organisms		Rate
	HPO4 [gP/m ³]	ALG [gDM/m ³]	
Growth of algae	$-\alpha_{P,ALG}$	1	$\rho_{gro,ALG}$
Death of algae		-1	$\rho_{death,ALG}$

Process Rates

$$\rho_{\text{gro,ALG}} = k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}}$$

$$\rho_{\text{death,ALG}} = k_{\text{death,ALG}} C_{\text{ALG}}$$

Transformation Rates

$$r_{\text{HPO}_4} = -\alpha_{\text{P,ALG}} \cdot k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}}$$

$$r_{\text{ALG}} = k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}} - k_{\text{death,ALG}} C_{\text{ALG}}$$

Mass Balance in Well-Mixed Epilimnion

$$\frac{d\mathbf{C}}{dt} = \frac{Q_{\text{in}}}{V} (\mathbf{C}_{\text{in}} - \mathbf{C}) + \frac{\mathbf{J}_{\text{int}}}{V} + \mathbf{r}$$

$$\mathbf{C} = \begin{pmatrix} C_{\text{HPO}_4} \\ C_{\text{ALG}} \end{pmatrix} \quad \mathbf{C}_{\text{in}} = \begin{pmatrix} C_{\text{HPO}_4, \text{in}} \\ 0 \end{pmatrix} \quad \mathbf{J}_{\text{int}} = \begin{pmatrix} 0 \\ 0 \end{pmatrix}$$

Mass Balance in Well-Mixed Epilimnion

$$\frac{dC}{dt} = \frac{Q_{\text{in}}}{V} (C_{\text{in}} - C) + \frac{J_{\text{int}}}{V} + \mathbf{r}$$

Differential Equations

$$\frac{dC_{\text{HPO}_4}}{dt} = \frac{Q_{\text{in}}}{V} (C_{\text{HPO}_4, \text{in}} - C_{\text{HPO}_4}) + r_{\text{HPO}_4}$$

$$\frac{dC_{\text{ALG}}}{dt} = -\frac{Q_{\text{in}}}{V} C_{\text{ALG}} + r_{\text{ALG}}$$

Differential Equations

$$\frac{dC_{\text{HPO}_4}}{dt} = \frac{Q_{\text{in}}}{V} \left(C_{\text{HPO}_4, \text{in}} - C_{\text{HPO}_4} \right) - \alpha_{\text{P,ALG}} \cdot k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}}$$

$$\frac{dC_{\text{ALG}}}{dt} = -\frac{Q_{\text{in}}}{V} C_{\text{ALG}} + k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}} - k_{\text{death,ALG}} C_{\text{ALG}}$$

Differential Equations

Example 11.1

$$\frac{dC_{\text{HPO}_4}}{dt} = \overbrace{\frac{Q_{\text{in}}}{V} (C_{\text{HPO}_4, \text{in}} - C_{\text{HPO}_4})}^{\text{net input via in/outflow}} \underbrace{- \alpha_{\text{P,ALG}} \cdot k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}}}_{\text{consumption by algae}}$$

$$\frac{dC_{\text{ALG}}}{dt} = \overbrace{-\frac{Q_{\text{in}}}{V} C_{\text{ALG}}}^{\text{loss via outflow}} + \overbrace{k_{\text{gro,ALG}} \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} C_{\text{ALG}}}_{\text{growth of algae}} \underbrace{- k_{\text{death,ALG}} C_{\text{ALG}}}_{\text{death of algae}}$$

Extended Process Rates

Additional influence factors of algae growth rate to account for yearly cycles in temperature and light.

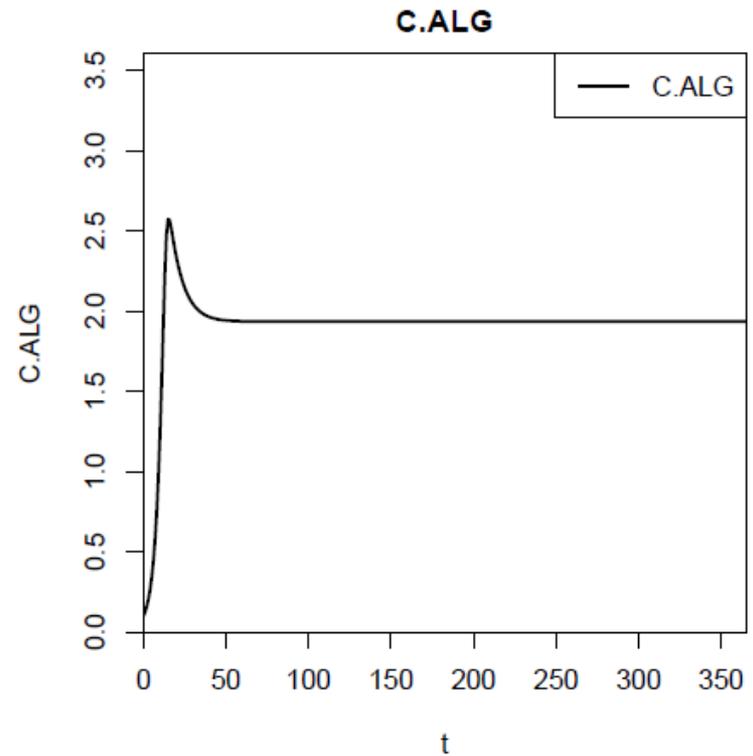
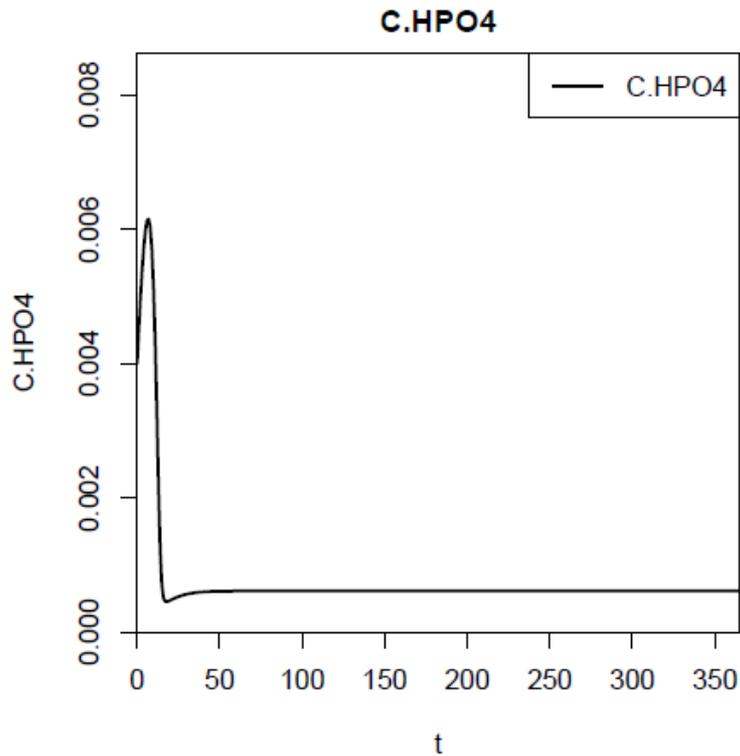
$$\rho_{\text{gro,ALG}} = k_{\text{gro,ALG}} \cdot \exp\left(\beta_{\text{ALG}}(T - T_0)\right) \cdot \frac{1}{\lambda h} \log\left(\frac{K_I + I_0}{K_I + I_0 \exp(-\lambda h)}\right) \cdot \frac{C_{\text{HPO}_4}}{K_{\text{HPO}_4} + C_{\text{HPO}_4}} \cdot C_{\text{ALG}}$$

Seasonally Varying Environmental Conditions

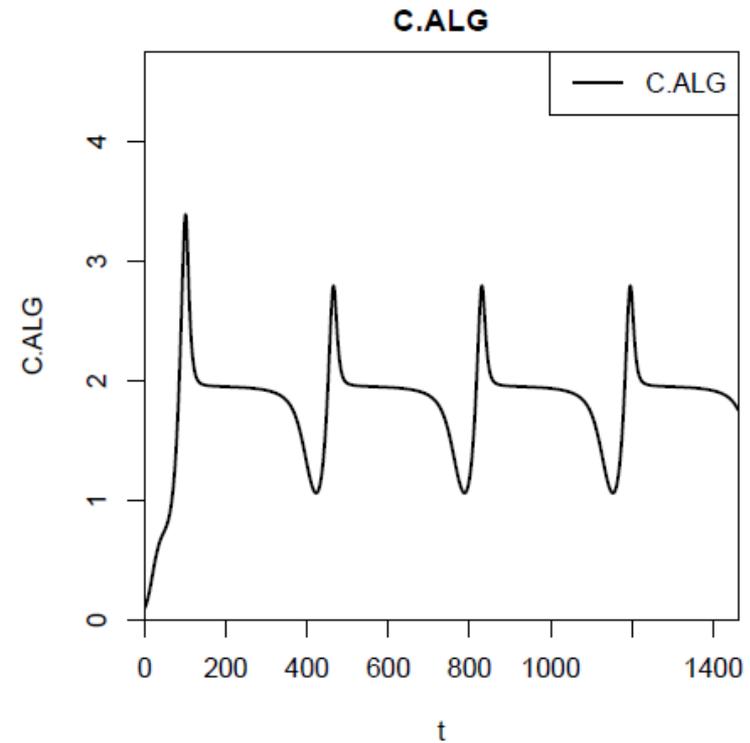
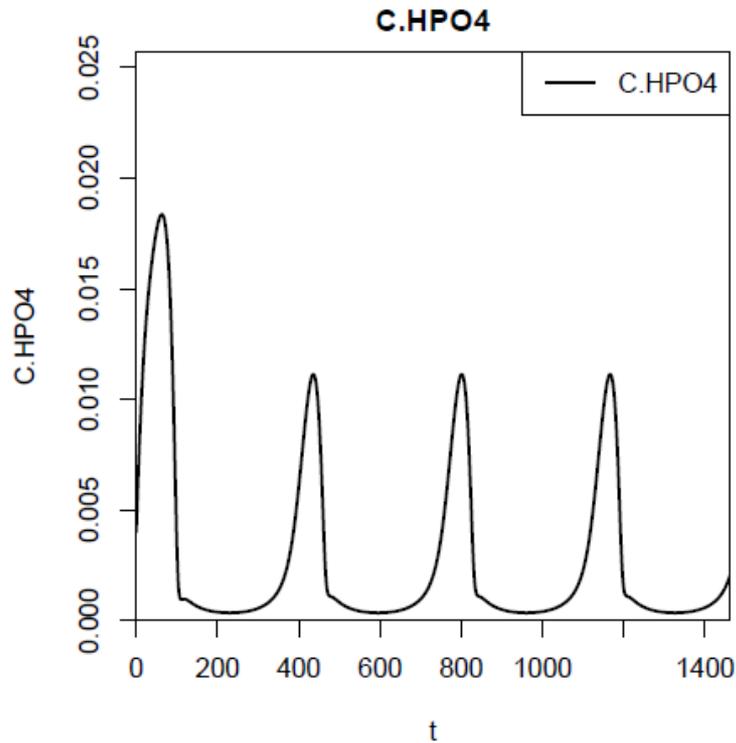
$$T(t) = \frac{T_{\max} + T_{\min}}{2} + \frac{T_{\max} - T_{\min}}{2} \cos \left(2\pi \frac{t - t_{\max}}{t_{\text{per}}} \right)$$

$$I_0(t) = \frac{I_{0,\max} + I_{0,\min}}{2} + \frac{I_{0,\max} - I_{0,\min}}{2} \cos \left(2\pi \frac{t - t_{\max}}{t_{\text{per}}} \right)$$

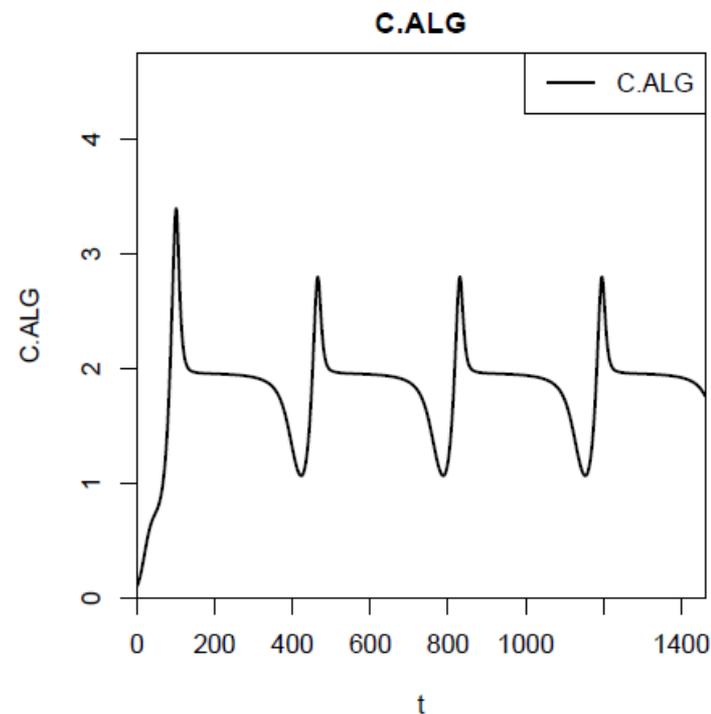
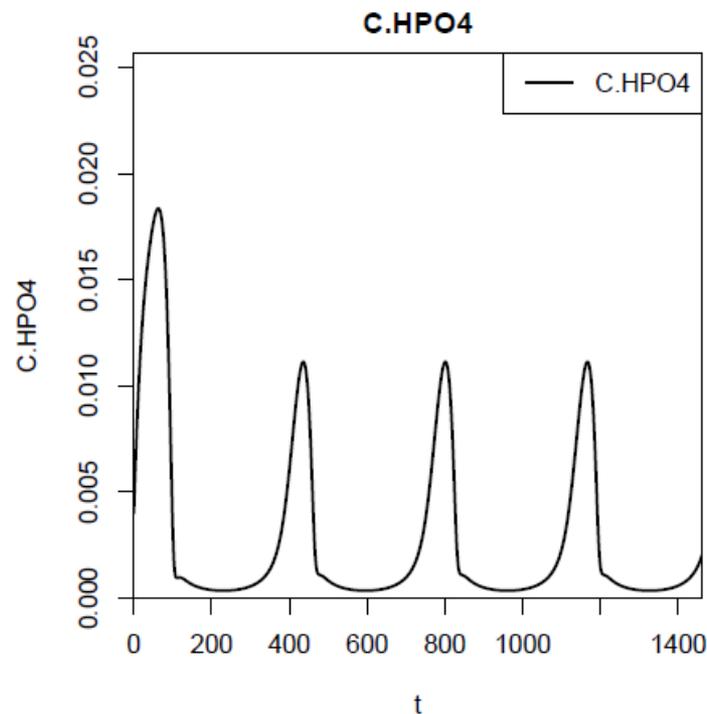
Results for constant environmental conditions



Results for periodic environmental conditions



- Acquire basic knowledge of the formulation of transport and transformation processes to formulate a simple lake plankton model.
- Become familiar with the process table notation and rate formulation that will be the basis of the more complex models.



1. Introduction, principles of modelling environmental systems, mass balance in a mixed reactor, process table notation, simple lake plankton model
Exercise: R, ecosim-package, simple lake plankton model
Exercise: lake phytoplankton-zooplankton model
2. Process stoichiometry Exercises: analytical solution, calculation with stoichcalc
3. Biological processes in lakes
4. Physical processes in lakes, mass balance in multi-box and continuous systems Exercise: structured, biogeochemical-ecological lake model
Assignments: build your own model by implementing model extensions
5. Physical processes in rivers, bacterial growth, river model for benthic populations Exercise: river model for benthic populations, nutrients and oxygen
6. Uncertainty, Parameter estimation, Stochasticity
Exercise: parameter estimation
Exercise: stochasticity, uncertainty
7. Existing models and applications in research and practice, examples and case studies, preparation of the oral exam, feedback

1. Install a current version of R and R-Studio and the `ecosim`-package on your notebook → see Program
2. If you are not very familiar with R, do the tutorial:
<https://cran.r-project.org/doc/contrib/Torfs+Brauer-Short-R-Intro.pdf>
3. Read chapter 11.1 about the first didactical model
4. Read chapters 16.1 and 16.2 about the `ecosim`-package.
5. Think about your open questions to ask them next week!