Puget Sound Regional Synthesis Model
Modeling Zooplankton, Phytoplankton, and Nutrients in Aquatic Systems

Improvement and enhancement of the existing one cell model and development of a new multi-cell model for simulating the full life cycle of plankton in Marine Systems

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Introduction

The marine environment is under a sustained threat from the consequences of human activities, including climate change, ozone depletion, toxic pollution and increasingly intensive fisheries. These threats to the marine environment threaten the entire web of life in the oceans, especially plankton, organisms that form the basis of all ocean food chains. Changes in the abundance and composition of plankton affect the stability of populations at higher levels in the food chain. To reduce the damage to the marine environment full life cycle models are being developed. The existing one-cell model and a newly created multi-cell model consist of the tools and techniques designed to understand and predict how physical, chemical and biological processes affect marine organisms, specifically different types of plankton. The original single-cell foodweb model did not consider a variety of oceanic processes that are required to properly simulate the full life cycle, so major changes to the model were essential. In the next section, these changes are further discussed. In addition, a new multi-cell model was developed to simulate the real environment by coupling the newly modified foodweb model (now called the Aquatic Bio-Chemical model or simply *ABC*) to a hydrodynamic model (The Princeton Ocean Model or *POM*). The POM-ABC model is discussed in the second section. Future development will include the coupling of the *ABC* model to other existing models, like the Environmental Fluid Dynamics Code (*EFDC*) model. The integration of different models will allow large-scale simulations of the marine environment in the Puget Sound basin.

PART I:
Improvement and Enhancement of the Original Foodweb Model

Since the original single-cell foodweb model did not take into account a wide range of oceanic processes that are required to properly simulate the full life cycle of the marine environment, major changes to the model were required. The following changes have been made: introduction of new coefficients, modification of the existing transfer processes, implementation of the fourth order Runge-Kutta method to solve differential equations (to calculate state variable equations), and creation of two other models—the chemostat model (to validate the one cell model) and the non-constant light model (to take into account the difference between seasons and time of the day). The rest of this section further discusses these changes.

Modification of the Existing Transfer Processes & Introduction of New Coefficients

Phytoplankton Respiration

An oxygen limitation term (a half saturation constant which refers to the level of oxygen at which the process would proceed at one half of its maximum rate) was added to the phytoplankton respiration transfer process. So in case when there is very low (or no) oxygen, the phytoplankton would limit their respiration, since there is little or no oxygen to breath with. See Appendix A for more information about this transfer process.

Phytoplankton Death

As in Phytoplankton Respiration, an oxygen limitation term was added to make the phytoplankton dye faster when there is low oxygen, since they cannot breath. See Appendix A for more information about this transfer process.

Zooplankton Grazing

An oxygen limitation term was added, so that the zooplankton do not eat when there is low oxygen. Since the zooplankton have to swim to catch their food, in case of low or no oxygen, they have too much difficulty breathing to swim and catch food. See Appendix A for more information about this transfer process.

Zooplankton Respiration

Two fundamental changes were made to the zooplankton respiration transfer process. One of them was oxygen limitation (similar to the Phytoplankton Respiration process). The second one was a basal respiration rate (or basal metabolism). This is a relatively slow rate that the zooplankton have to breath at to stay alive, if they were doing nothing else. This means that if there is no food, they will slowly starve. See Appendix A for more information about this transfer process.

Zooplankton Egestion

Zooplankton egestion is the stuff the zooplankton get rid of from their gut, or a portion of their food that they cannot digest. The modified egestion function in the single-cell model works by first using user input coefficients to obtain the fraction of their total food that they cannot digest. It then calculates how much (if any) of the food is indigestible from a stoichiometric perspective. Thus the model forces that the food absorbed (digested) by the zooplankton must have the same overall stoichiometry as the zooplankton themselves. This is because the model converts absorbed food directly into zooplankton biomass (i.e. more or bigger zooplankton). Whatever food is indigestible is partitioned to the organic pools (DOM/LPOM/RPOM) using the ratio of the coefficients entered by the user.

Zooplankton Mortality

This transfer process is very similar to the Phytoplankton Death transfer process. See Appendix A for more information about the zooplankton mortality transfer process.

Bacterial Respiration for RPOM

While bacteria do not have lungs, the term “respiration” is used for the biological process that transforms oxygen into energy. Bacteria make their living combining compounds and extracting the energy released in the reaction. The original single-cell model only considered bacteria that combine DOM (Dissolved Organic Matter), LPOM (Labile Particulate Organic Matter) and oxygen (the respiration part) to produce CO2 (or other hydrocarbons). However, RPOM (Refractory Particulate Organic Matter) was not taken into account. Therefore, in the modified single-cell model this process has been added. See Appendix A for more information about this transfer process.

Bacterial Remineralization

This process requires oxygen, so an oxygen limitation term was added to slow the remineralization process in the absence of oxygen. See Appendix A for more information about this transfer process.

Temperature Dependence Function/Coefficients

Zooplankton and phytoplankton do not have internal temperature regulation (similar to cold-blooded animals, like snakes, frogs, etc.). Thus, they depend on external conditions (for example, when the temperature drops their bodily functions slow down). The temperature dependence function adjusts the following coefficients $\mu_{o}i$, I_{max}, Ch, Cp, Cm, Cn, Cz, Cd, Ce and Cf, which regulate the internal functions of phytoplankton and zooplankton, according to the external temperature. See “Constants and coefficients” in Appendix A for the description of the coefficients.

Fixed/Proportional Feature

The original single-cell model used a fixed stoichiometry for the bacterial remineralization of organic matter, which means that bacteria consume the elements (C, N, P) in organic matter in a certain, fixed ratio. However, it was discovered that the phytoplankton/zooplankton that contribute to the organic pools often did so in ratios other than what the bacteria used. So a “proportional” option was developed, where the bacteria would use the elements in the organic pools in whatever ratio exists. The applet allows the user to select one of these two options. Depending on the selected option, the model either uses the ratio entered through the applet (“fixed” option) or calculates it itself (“proportional” option).

Runge-Kutta

In the original model a state variable equation was a first-order differential equation parameterized by transfer processes. In order to increase the precision of calculations, it has been changed to the fourth order Runge-Kutta method, which is one of the standard algorithms to solve differential equations. The fourth order Runge-Kutta method provides an excellent balance of power, precision and at the same time simplicity to the model.

The fourth order Runge-Kutta requires four gradient or "k" terms to calculate y_{n+1}

$$y_{n+1} = y_n + \frac{1}{6}(k_1 + 2k_2 + 2k_3 + k_4)$$

$$k_1 = hf(t_n,\ y_n), \qquad k_2 = hf(t_n + \frac{h}{2},\ y_n + \frac{k_1}{2})$$

$$k_3 = hf(t_n + \frac{h}{2},\ y_n + \frac{k_2}{2}), \qquad k_4 = hf(t_n + h,\ y_n + k_3)$$

The algorithm of the modified model follows:

```
Start with state variables at the beginning of timestep (original value)
Evaluate derivative of all the state variables (as was done in the original model)
Calculate k1 = timestep*derivative (for each state variable)
Save these values
Increment all state variables so than new value  = original value + k1/2
Evaluate derivative of all the state variables, using new updated values
Calculate k2 = timestep*derivative (for each state variable)
Save these values
Increment all state variables so than new value = original value + k2/2
Evaluate derivative of all the state variables, using new updated values
Calculate k3 = timestep*derivative (for each state variable)
Save these values
Increment all state variables so than new value = original value + k3
Evaluate derivative of all the state variables, using new updated values
Calculate k4 = timestep*derivative (for each state variable)
Save these values
Calculate new value = original value + 1/6*(k1 + 2k2 + 2k3 + k4)
```

Non-Constant Light Model vs. Constant Light

The original single-cell model considered light as a constant value, which means it made no difference between day and night, winter and summer, etc. The modified model has an additional feature that allows the user to switch between constant and non-constant light. If the user chooses the non-constant light option on the main page of the applet, then he is asked to enter the start time (as a decimal value, i.e. 0 = January 1, 1=January 2, etc.) and the latitude. These parameters are used to calculate the light at each time step. See Appendix B for differences in growth for non-constant light vs. constant light.

ChemoStat Model

The chemostat validates the one cell model and determines the various coefficients by creating steady-state conditions. If a chemical or biological reaction occurs in a closed system (like the single cell model), whatever is being consumed in the reaction (nutrients, etc.) gets depleted and the reaction stops. And in order to figure out how fast the reaction takes place, many parameters need to be measured in time.

The chemostat allows a continual inflow of reactants (nutrients, etc.) into the cell, so they do not get completely depleted. Thus after a start-up time, the reaction will continue at some rate determined by how much is being added to the cell. Then balancing what is coming in with what goes out, the reaction rate can be calculated. In the case with one cell model, the reaction may be phytoplankton growing, or zooplankton eating phytoplankton, or basically any of the transfer processes.

Currently, the user can choose which model to execute (i.e., the *ABC* model or the Chemostat model) from the main page of the applet. In order to implement the Chemostat model, a new class called ChemoStat was added to the current hierarchy. This class contains a flow rate parameter (which is measured in units of volume per day, where volume is the volume of the WaterCell) and boundary conditions for the mass of each WaterComponent (phytoplankton, zooplankton, DOM, LPOM, RPOM, NO3, NH4, PO4 and O2) of the WaterCell. These parameters are entered by the user through the applet. At each time step the Chemostat model updates the components of the WaterCell. The results of the Chemostat model are outputted in a similar fashion to the results of the *ABC* model and could be viewed by a variety of data analysis applications like MatLab or Microsoft Excel.

Applet Modifications

Due to the above-mentioned changes, the applet (through which the user inputs all coefficients) had to be modified as well. Many coefficients were removed from the applet because they were either not used by the model at all or were not supposed to be entered by the user (since they were calculated by the model). On another hand, several new coefficients were added to the applet (like, basal metabolism, which was discussed earlier as well as half saturation constants, constants for light, etc.). In addition, the general layout of the applet got changed. Instead of choosing from the drop down menu which type of zooplankton or phytoplankton to modify, the applet displays the coefficients for all types at the same time, which allows the user to modify all values at once. Units were added to every field on the applet, so that way it is much easier for the user to figure out the correct quantity of each coefficient. Also an additional page was added to the applet, to enter coefficients for the chemostat model.

These and any future changes could be viewed on http://coisa.ocean.washington.edu/foodweb/ (click the “Applet” link on the left side of the page, then enter “guest” for both username and password to view the applet).

Part II

Development of a New Multi-Cell Model

POM-ABC Model

The Princeton Ocean Model (*POM*) is being used to model the circulation of water in the ocean basin. This model was developed in Fortran, so in order to integrate the *POM* model and the *ABC* model, an interface between C++ and Fortran had to be developed. Cfortran.h was chosen as an easy-to-use powerful bridge between C/C++ and

Fortran. This interface is easily created with little or no knowledge of any machine, OS, compiler or linker subtleties. The description of the routines (i.e., the routines' arguments and its return value) is sufficient enough for cfortran.h to create the interface and there are no special preprocessors or other programs needed (see http://wwwinfo.cern.ch/asd/cernlib/cfortran.html for further details). The *POM* model calls the *ABC*'s routines through the interface provided by cfortran.h. Then the *POM* model receives the data from the *ABC* model, which includes the mass of each WaterComponent (phytoplankton, zooplankton, DOM, LPOM, RPOM, NO3, NH4, PO4 and O2) of the WaterCell, and uses it for its calculations. The results are later outputted to a text file and could be viewed in a similar fashion to the results provided by the *ABC* model. The newly created interface helped to develop the first version of a multi-cell model, however the main advantage of this interface is its reusability, that is an ability to link the *ABC* model to any other Fortran models with no additional coding (like the Environmental Fluid Dynamics Code Model or *EFDC*, which is another hydrodynamic model).

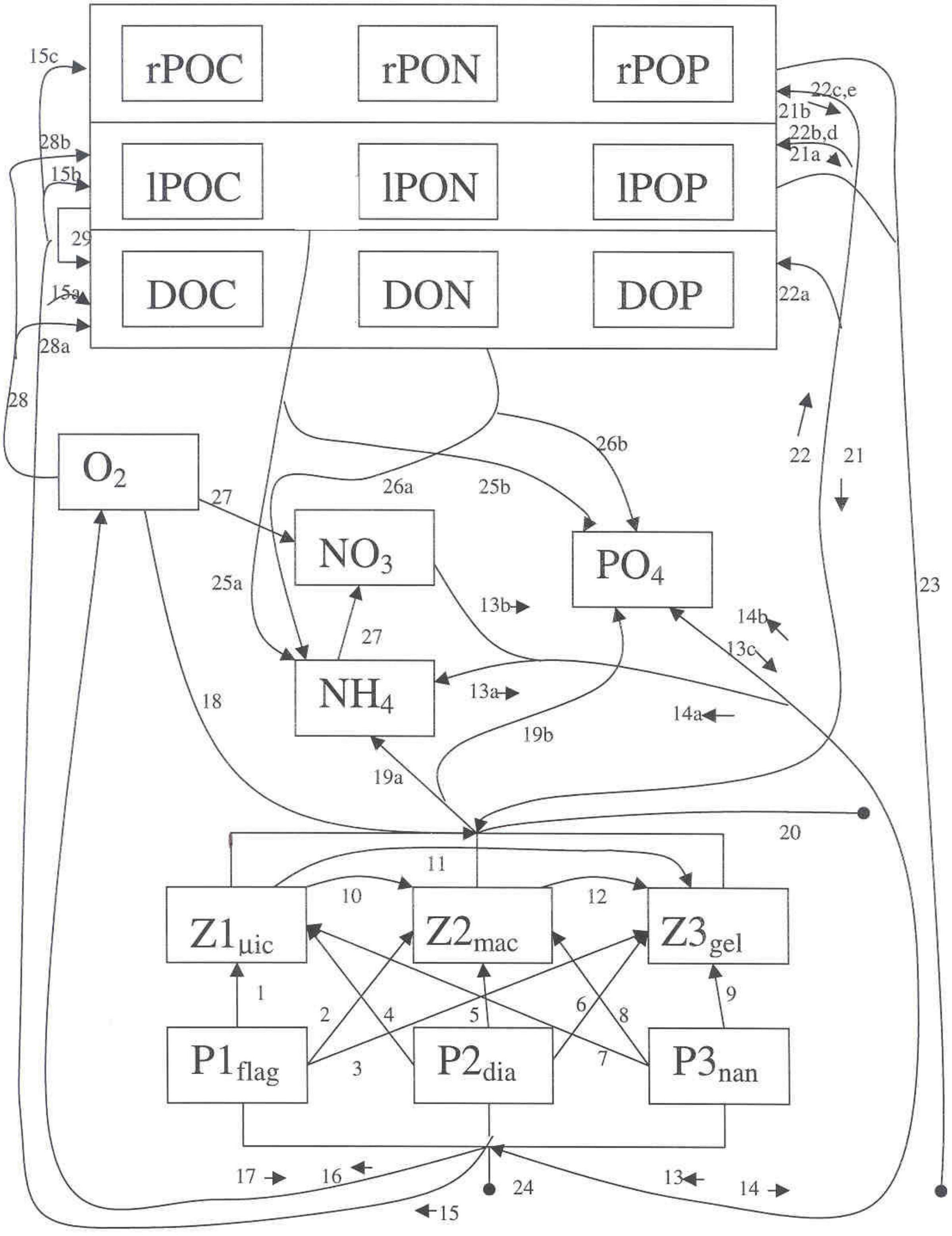
Conclusion

The project on improvement and enhancing of the existing one cell model and development of a new multi-cell model for simulating the full life cycle of plankton in Marine Systems has been successfully accomplished. The newly created model has shown a remarkable ability to simulate and predict physical, chemical and biological processes, which affect marine organisms, and particularly different types of plankton. Encapsulating testing modules (like the ChemoStat model in this project) in large-scale applications to validate closed systems (like the single cell model) dramatically increases precision of the output. The detailed information of the model, documentation and future work can be found on http://coisa.ocean.washington.edu/foodweb/.

Future Work

Work on an XMLInput class is in progress and expected to be completed soon. Additional future work will also include an implementation of "Scheduler", a system (possibly written in Java), which would allow several linked models to run at the same time (like *POM-ABC*, *EFDC-ABC*, or any other combination) and be able to send data from one model to another one through some common API. See Appendix C for details. Blue squares represent the API that should be similar for all models. The dashed line between the *ABC* model and the *POM* model represents the *POM-ABC* model discussed earlier.

Appendix A: Model Design



Arrow definitions:

1-9. Herbivorous grazing ($\mathbf{hg}_{\mathbf{P-Z}}$)

10-12. Carnivorous grazing ($\mathbf{cg}_{\mathbf{Z-Z}}$)

13. Nutrient uptake by phytoplankton
    a. of NH4 ($\mathbf{nu}_{\mathbf{NH4-P}}$)
    b. of NO3 ($\mathbf{nu}_{\mathbf{NO3-P}}$)
    c. of PO4 ($\mathbf{nu}_{\mathbf{PO4-P}}$)
14. Nutrient excretion from phytoplankton
    a. of NH4 ($\mathbf{ne}_{\mathbf{P-NH4}}$)
    b. of PO4 ($\mathbf{ne}_{\mathbf{P-PO4}}$)
15. Release from phytoplankton
    a. Exudation, to DOM ($\mathbf{pe}_{\mathbf{P-DOC}}$, $\mathbf{pe}_{\mathbf{P-DON}}$, $\mathbf{pe}_{\mathbf{P-DOP}}$)
    b. Death, to lPOM ($\mathbf{pd}_{\mathbf{P-lPOC}}$, $\mathbf{pd}_{\mathbf{P-lPON}}$, $\mathbf{pd}_{\mathbf{P-lPOP}}$)
    c. Death, to rPOM ($\mathbf{pd}_{\mathbf{P-rPOC}}$, $\mathbf{pd}_{\mathbf{P-rPON}}$, $\mathbf{pd}_{\mathbf{P-rPOP}}$)
16. Photosynthesis ($\mathbf{ps}_{\mathbf{P-O2}}$)
17. Phytoplankton respiration ($\mathbf{pr}_{\mathbf{O2-P}}$)
18. Zooplankton respiration ($\mathbf{zr}_{\mathbf{O2-Z}}$)
19. Nutrient excretion from zooplankton
    a. of NH4 ($\mathbf{nx}_{\mathbf{Z-NH4}}$)
    b. of PO4 ($\mathbf{nx}_{\mathbf{Z-PO4}}$)
20. Predation on zooplankton (OUT) ($\mathbf{zp}_{\mathbf{Z-out}}$)
21. Detrital grazing
    a. of lPOM ($\mathbf{dg}_{\mathbf{lPOC-Z}}$, $\mathbf{dg}_{\mathbf{lPON-Z}}$, $\mathbf{dg}_{\mathbf{lPOP-Z}}$)
    b. of rPOM ($\mathbf{dg}_{\mathbf{rPOC-Z}}$, $\mathbf{dg}_{\mathbf{rPON-Z}}$, $\mathbf{dg}_{\mathbf{rPOP-Z}}$)
22. Release from zooplankton
    a. Exudation, to DOM ($\mathbf{zd}_{\mathbf{Z-DOC}}$, $\mathbf{zd}_{\mathbf{Z-DON}}$, $\mathbf{zd}_{\mathbf{Z-DOP}}$)
    b. Mortality, to lPOM ($\mathbf{zm}_{\mathbf{Z-lPOC}}$, $\mathbf{zm}_{\mathbf{Z-lPON}}$, $\mathbf{zm}_{\mathbf{Z-lPOP}}$)
    c. Mortality, to rPOM ($\mathbf{zm}_{\mathbf{Z-rPOC}}$, $\mathbf{zm}_{\mathbf{Z-rPON}}$, $\mathbf{zm}_{\mathbf{Z-rPOP}}$)
    d. Egestion to lPOM ($\mathbf{ze}_{\mathbf{Z-lPOC}}$, $\mathbf{ze}_{\mathbf{Z-lPON}}$, $\mathbf{ze}_{\mathbf{Z-lPOP}}$)
    e. Egestion to rPOM ($\mathbf{ze}_{\mathbf{Z-rPOC}}$, $\mathbf{ze}_{\mathbf{Z-rPON}}$, $\mathbf{ze}_{\mathbf{Z-rPOP}}$)
23. Detrital sinking (OUT) ($\mathbf{ds}_{\mathbf{lPOC-out}}$, $\mathbf{ds}_{\mathbf{lPON-out}}$, $\mathbf{ds}_{\mathbf{lPOP-out}}$, $\mathbf{ds}_{\mathbf{rPOC-out}}$, $\mathbf{ds}_{\mathbf{rPON-out}}$, $\mathbf{ds}_{\mathbf{rPOP-out}}$)
24. Cell sinking (OUT) ($\mathbf{cs}_{\mathbf{P-out}}$)
25. Bacterial remineralization of lPOM
    a. to NH4 ($\mathbf{bm}_{\mathbf{lPON-NH4}}$)
    b. to PO4 ($\mathbf{bm}_{\mathbf{lPOP-PO4}}$)
    c. to CO2 (not shown; $\mathbf{bm}_{\mathbf{lPOC-CO2}}$)
26. Bacterial remineralization of DOM
    a. to NH4 ($\mathbf{bm}_{\mathbf{DON-NH4}}$)
    b. to PO4 ($\mathbf{bm}_{\mathbf{DOP-PO4}}$)
    c. to CO2 (not shown; $\mathbf{bm}_{\mathbf{DOC-CO2}}$)
27. Nitrification ($\mathbf{ni}_{\mathbf{NH4-NO3}}$, $\mathbf{ni}_{\mathbf{O2-NO3}}$)
28. Bacterial respiration
    a. of DOC ($\mathbf{br}_{\mathbf{O2-DOC}}$)
    b. of lPOC ($\mathbf{br}_{\mathbf{O2-lPOC}}$)
29. Solublization/bacterial degradation of lPOM to DOM ($\mathbf{so}_{\mathbf{lPOC-DOC}}$, $\mathbf{so}_{\mathbf{lPON-DON}}$, $\mathbf{so}_{\mathbf{lPOP-DOP}}$)
30. Bacterial remineralization of rPOM
    a. to NH4 ($\mathbf{bm}_{\mathbf{rPON-NH4}}$)
    d. to PO4 ($\mathbf{bm}_{\mathbf{rPOP-PO4}}$)
    e. to CO2 (not shown; $\mathbf{bm}_{\mathbf{rPOC-CO2}}$)

State Variable Equations:

P1, P2, P3

$dP\mathit{i}/dt = ps_{\mathrm{P\text{-}O2}} - pr_{\mathrm{O2\text{-}P}} - hg_{\mathrm{P\text{-}Z}} - pe_{\mathrm{P\text{-}DOM}} - pd_{\mathrm{P\text{-}r,lPOM}} - cs_{\mathrm{P\text{-}out}}$

Z1, Z2, Z3

$dZ\mathit{i}/dt = -zr_{\mathrm{O2\text{-}Z}} - zd_{\mathrm{Z\text{-}DOM}} - ze_{\mathrm{Z\text{-}r,lPOM}} - zp_{\mathrm{Z\text{-}out}} - zm_{\mathrm{Z\text{-}r,lPOM}} + zg_{\mathrm{[P,Z,r,lDOM]\text{-}Z}} - cg_{\mathrm{Z\text{-}Z}} + zs_{\mathrm{Z\text{-}Z}}$

NH_4

$dNH_4/dt = \mathrm{stoich(N{:}C)}[ne_{\mathrm{P\text{-}NH4}} + nx_{\mathrm{Z\text{-}NH4}} + bm_{\mathrm{[DOM,r,lPOM]\text{-}NH4}} - nu_{\mathrm{NH4\text{-}P}} - ni_{\mathrm{NH4\text{-}NO3}}]$

NO_3

$dNO_3/dt = \mathrm{stoich(N{:}C)}[ni_{\mathrm{NH4\text{-}NO3}} - nu_{\mathrm{NO3\text{-}P}}]$

{airborne deposition, precipitation at surface}

PO_4

$dPO_4/dt = \mathrm{stoich(P{:}C)}\ [ne_{\mathrm{P\text{-}PO4}} + nx_{\mathrm{Z\text{-}PO4}} + bm_{\mathrm{[DOM,r,lPOM]\text{-}PO4}} - nu_{\mathrm{PO4\text{-}P}}]$

O_2

$dO_2/dt = \mathrm{stoich(O{:}C)}\ [ps_{\mathrm{P\text{-}O2}} - pr_{\mathrm{O2\text{-}P}} - zr_{\mathrm{O2\text{-}Z}} - br_{\mathrm{O2\text{-}DOC,lPOC}}] - [ni_{\mathrm{O2\text{-}NO3}}]$

{O_2 *boundary conditions:* $z=0$: $G/h\ (O_2sat - O_2)$
$z=h$: $D(O_2water - O_2\ sed)$}

DOC, DON, DOP[1]

$dDOM/dt = pe_{\mathrm{P\text{-}DOM}} + zd_{\mathrm{Z\text{-}DOM}} + so_{\mathrm{lPOM\text{-}DOM}} - bm_{\mathrm{DOM\text{-}[CO2,NH4,PO4]}}$

lPOC, lPON, lPOP[1]

$d\ lPOM/dt = ze_{\mathrm{Z\text{-}lPOM}} + zm_{\mathrm{Z\text{-}lPOM}} + pd_{\mathrm{P\text{-}lPOM}} - ds_{\mathrm{lPOM\text{-}out}} - dg_{\mathrm{lPOM\text{-}Z}} - so_{\mathrm{lPOM\text{-}DOM}} - bm_{\mathrm{lPOM\text{-}[CO2,NH4,PO4]}}$

rPOC, rPON, rPOP[1]

$d\ rPOM/dt = ze_{\mathrm{Z\text{-}rPOM}} + zm_{\mathrm{Z\text{-}rPOM}} + pd_{\mathrm{P\text{-}rPOM}} - ds_{\mathrm{rPOM\text{-}out}} - dg_{\mathrm{rPOM\text{-}Z}} - bm_{\mathrm{rPOM\text{-}[CO2,NH4,PO4]}}$

[1] equations for DON, rPON, lPON have stoich(N:C);
equations for DOP, rPOP, lPOP have stoich(P:C)

Transfer Processes: *all must be ≥ 0*

ps: photosynthesis (16)

from Pi to O_2

$$ps_{P\text{-}O2} = P\mathit{i}\ \mu_o\mathit{i}\ e^{R\mathit{i}T}\ \min\{1 - e^{-E}k^{\mathit{i}/E},\ rnu_N,\ rnu_P\}\ /\ \text{stoich}(C{:}O)_1$$

where: $\mu_o i$ = maximal growth rate for P*i* = $\mu_o i_{Tbase} * e^{-Ri*Tbase}$
$\mu_o i_{Tbase}$ = maximal growth rate for P*i* at *Tbase*
Tbase = base temperature
R*i* = temperature growth coefficient for P*i*
T = temperature (input)
$E_k i$ = light saturation coefficient for P*i*
E = light (input)

pr: phytoplankton respiration (17)

from O_2 to Pi

$$pr_{O2\text{-}P} = P\mathit{i}\ *\ Cq\ /\ \text{stoich}(C{:}O)_2\ *\ \frac{O_2}{K_{i\,O2} + O_2}$$

where: *Cq* is a constant for phytoplankton respiration
$K_{i\,O2}$ is a half saturation constant for P*i* on O_2

nu: nutrient uptake (13a, b, c)

from NO_3, NH_4, PO_4 to Pi

$$nu_{NO3\text{-}P} = ps\ /\ \text{stoich}(C{:}N)_1\ *\ \frac{rnu_{NO3}}{rnu_{NH4} + rnu_{NO3}}$$

$$nu_{NH4\text{-}P} = ps\ /\ \text{stoich}(C{:}N)_2\ *\ \frac{rnu_{NH4}}{rnu_{NH4} + rnu_{NO3}}$$

$$nu_{PO4\text{-}P} = ps\ /\ \text{stoich}(C{:}P)_1$$

where: $rnu_N = rnu_{NH4} + rnu_{NO3}$
$rnu_P = rnu_{PO4}$

$$rnu_{NH4} = \frac{NH_4}{K_{i\,NH4} + NH_4}$$

$$rnu_{NO3} = \frac{NO_3}{K_{i\,NO3} + NO_3}\ *\ \frac{K_{i\,NH4}}{K_{i\,NH4} + NH_4}$$

K_i[nutr] = half saturation constant for P*i* on nutrient [NO_3, NH_4, PO_4]

ne: nutrient excretion from phytoplankton (14a, b)

from Pi to NH_4, PO_4

$ne_{P\text{-}NH4} = pr\ /\ \text{stoich}(C{:}N)_3$
$ne_{P\text{-}PO4} = pr\ /\ \text{stoich}(C{:}P)_2$

pe: phytoplankton exudation (15a)

from Pi to DOM

$pe_{\text{P-DOC}} = Pi * Cx$ *where:* Cx is a constant for exudation

$pe_{\text{P-DON}} = Pi * Cx \, / \, \text{stoich}(C{:}N)_4$

$pe_{\text{P-DOP}} = Pi * Cx \, / \, \text{stoich}(C{:}P)_3$

pd: phytoplankton death (15b, c)

from Pi to (lPOM+rPOM)

if $(Cl + Cr) \neq 0$:

$$pd_{\text{P-lPOM}} = Pi * Cl + Pi * Cq * \frac{K_{i\,O2} + O_2}{O_2} * \frac{Cl}{Cl + Cr}$$

where:
Cl is a constant for death to labile pool
Cq is a constant for phyto. respiration
$K_{i\,O2}$ is a half saturation constant for Pi on O_2

$$pd_{\text{P-rPOM}} = Pi * Cr + Pi * Cq * \frac{K_{i\,O2} + O_2}{O_2} * \frac{Cr}{Cl + Cr}$$

where:
Cr is a const. for death to refractory pool
Cq is a constant for phyto. respiration
$K_{i\,O2}$ is a half saturation constant for Pi on O_2

otherwise:

$$pd_{\text{P-lPOM}} = Pi * Cq * \frac{K_{i\,O2} + O_2}{O_2}$$

where: Cq is a constant for phytoplankton respiration
$K_{i\,O2}$ is a half saturation constant for Pi on O_2

$pd_{\text{P-rPOM}} = 0$

and where:
to lPOC and rPOC are as written
to lPON have " / $\text{stoich}(C{:}N)_5$" and to rPON have " / $\text{stoich}(C{:}N)_6$"
to lPOP have " / $\text{stoich}(C{:}P)_4$" and to rPOP have " / $\text{stoich}(C{:}P)_5$"

cs: cell sinking (24)

from Pi to out

$cs_{\text{P-out}} = -d/dz\,(w_{phy}\,Pi)$ *where:* w_{phy} = a depth-varying sinking rate for phytoplankton

zg: zooplankton grazing (1-12, 21a,b)

from (lPOM + rPOM + Pi + Zi) to Zi

$zg = dg + cg + hg$

hg: herbivorous grazing (1-9)

from Pi to Zi; i = 1-3; j = 1-3

$$hg_{P\text{-}Z} = P1g + P2g + P3g \qquad Pig = Zj \; * \; \frac{\max(B - Co, 0)}{K_{iA} + B} \; * \; \frac{\phi j\, Pi}{A} \; * \; I_{max} \; * \; fz(T) \; * \; \frac{O_2}{K_{iO2} + O_2}$$

where:

I_{max} = maximal ingestion rate = $I_{maxTbase} * e^{-fz(T)*Tbase}$
$I_{maxTbase}$ = maximal ingestion rate at *Tbase*
Tbase = base temperature
Co = feeding threshold level, below which no grazing occurs
ϕj = preference for prey type, *j*=1-8: 1=P1, 2=P2, 3=P3, 4=Z1, 5=Z2, 6=Z3, 7=lPOM, 8=rPOM
K_{iA} = half-saturation constant for total food
K_{iO2} = half saturation constant for Z*i* on O_2
A = total food available
= $\phi1*P1 + \phi2*P2 + \phi3*P3 + \phi4*Z1 + \phi5*Z2 + \phi6*Z3 + \phi7*lPOM + \phi8*rPOM$
B = total food
= P1 + P2 + P3 + Z1 + Z2 + Z3 + lPOM + rPOM

cg: carnivorous grazing (10-12)

from Zi to Zi; i = 1-3; j =1-3

$$cg_{Z\text{-}Z} = Z1g + Z2g + Z3g \qquad Zig = Zj \; * \; \frac{\max(B - Co, 0)}{K_{iA} + B} \; * \; \frac{\phi j\, Zi}{A} \; * \; I_{max} \; * \; fz(T) \; * \; \frac{O_2}{K_{iO2} + O_2}$$

dg: detrital grazing (21a, b)

from lPOM, rPOM to Zi; i = 1-3; j =1-3

$$dg_{\,lPOM\text{-}Z} = Zj \; * \; \frac{\max(B - Co, 0)}{K_{iA} + B} \; * \; \frac{\phi j\, lPOM}{A} \; * \; I_{max} \; * \; fz(T) \; * \; \frac{O_2}{K_{iO2} + O_2}$$

$$dg_{\,rPOM\text{-}Z} = Zj \; * \; \frac{\max(B - Co, 0)}{K_{iA} + B} \; * \; \frac{\phi j\, rPOM}{A} \; * \; I_{max} \; * \; fz(T) \; * \; \frac{O_2}{K_{iO2} + O_2}$$

where:

from lPOC and rPOC are as written
from lPON have " / stoich$(C:N)_8$" and to rPON have " / stoich$(C:N)_9$"
from lPOP have " / stoich$(C:P)_7$" and to rPOP have " / stoich$(C:P)_8$"

zr: zooplankton respiration (18)

from O_2 to Zi

$$zr_{O2\text{-}Z} = f_z(T)\,(zg * Cz + Zi * Ch \; * \; \frac{O_2}{K_{iO2} + O_2}\;) \; / \; \text{stoich}(C:O)_3$$

where: *Cz* is a constant for zooplankton respiration = $Cz_{Tbase} * e^{-fz(T)*Tbase}$
Cz_{Tbase} = zooplankton respiration at *Tbase*
Ch is a constant for basal metabolism = $Ch_{Tbase} * e^{-fz(T)*Tbase}$
Ch_{Tbase} = basal metabolism at *Tbase*
Tbase = base temperature
K_{iO2} is a half saturation constant for Z*i* on O_2
$f_z(T)$ is a temperature coefficient

zs: zooplankton swimming

within any Zi, among depth boxes

$zs_{Z\text{-}Z} = -d/dz\,(w_{zoo}\, Zi)$ *where:* w_{zoo} = a depth-varying movement rate for zooplankton

nx: nutrient excretion from zooplankton (19a, b)

from Zi to NH_4, PO_4

$nx_{Z\text{-}NH4} = zr / \text{stoich}(C{:}N)_7$
$nx_{Z\text{-}PO4} = zr / \text{stoich}(C{:}P)_6$

zd: zooplankton exudation (22a)

from Zi to DOM

$zd_{Z\text{-}DOC} = f_z(T)\ zg * Cd$
$zd_{Z\text{-}DON} = f_z(T)\ zg * Cd / \text{stoich}(C{:}N)_{10}$
$zd_{Z\text{-}DOP} = f_z(T)\ zg * Cd / \text{stoich}(C{:}P)_9$

where: *Cd* is a constant for zooplankton exudation
$Cd = Cd_{Tbase} * e^{-fz(T)*Tbase}$
Cd_{Tbase} = zooplankton exudation at *Tbase*
Tbase = base temperature

ze: zooplankgon egestion (22d, e)

from Zi to (lPOM + rPOM)

$ze_{Z\text{-}lPOM} = f_z(T)\ zg * Ce$ *where:* *Ce* is a constant for zooplankton egestion to labile pool
$Ce = Ce_{Tbase} * e^{-fz(T)*Tbase}$
Ce_{Tbase} = zooplankton egestion to labile pool at *Tbase*
Tbase = base temperature

$ze_{Z\text{-}rPOM} = f_z(T)\ zg * Cf$ *where:* *Cf* is a constant for zooplankton egestion to refractory pool
$Cf = Cf_{Tbase} * e^{-fz(T)*Tbase}$
Cf_{Tbase} = zooplankton egestion to refractory pool at *Tbase*
Tbase = base temperature

and where: to lPOC and rPOC are as written
to lPON have "/ stoich(C:N)$_{13}$" and to rPON have "/ stoich(C:N)$_{14}$"
to lPOP have "/ stoich(C:P)$_{12}$" and to rPOP have "/ stoich(C:P)$_{13}$"

zm: zooplankton mortality (22b, c)

from Zi to (lPOM + rPOM)

if $(Cm + Cn) \neq 0$:

$$zm_{Z\text{-}lPOM} = Zi\, f_z(T) * Cm + Zi\, f_z(T) * Ch * \frac{K_{i\,O2}}{K_{i\,O2} + O_2} * \frac{Cm}{Cn + Cm}$$

where: *Cm* is a constant for zooplankton death to labile pool
$Cm = Cm_{Tbase} * e^{-fz(T)*Tbase}$
Cm_{Tbase} = zooplankton death to labile pool at *Tbase*
Ch is a constant for basal metabolism = $Ch_{Tbase} * e^{-fz(T)*Tbase}$
Ch_{Tbase} = basal metabolism at *Tbase*
Tbase = base temperature
K_{iO2} is a half saturation constant for Z*i* on O_2

$$zm_{Z\text{-}rPOM} = Zi\, f_z(T) * Cn + Zi\, f_z(T) * Ch * \frac{K_{i\,O2}}{K_{i\,O2} + O_2} * \frac{Cn}{Cm + Cn}$$

where: Cn is a constant for zooplankton death to refractory pool
$Cn = Cn_{Tbase} * e^{-fz(T)*Tbase}$
Cn_{Tbase} = zooplankton death to refractory pool at *Tbase*
Ch is a constant for basal metabolism = $Ch_{Tbase} * e^{-fz(T)*Tbase}$
Ch_{Tbase} = basal metabolism at *Tbase*
Tbase = base temperature
K_{iO2} is a half saturation constant for Zi on O_2

otherwise:

$$zm_{Z\text{-}lPOM} = Zi\, f_z(T) * Ch * \frac{K_{i\,O2}}{K_{i\,O2} + O_2}$$

$$zm_{Z\text{-}rPOM} = Zi\, f_z(T) * Ch * \frac{K_{i\,O2}}{K_{i\,O2} + O_2}$$

and where: to lPOC and rPOC are as written
to lPON have "/ $stoich(C:N)_{11}$" and to rPON have "/ $stoich(C:N)_{12}$"
to lPOP have "/ $stoich(C:P)_{10}$" and to rPOP have "/ $stoich(C:P)_{11}$"

zp: predation on zooplankton (20)

from Zi to out

$$zp_{Z\text{-}out} = Zi\, f_z(T) * Cp \quad \textbf{(module 1)}$$

$$zp_{Z\text{-}out} = Zi^2 f_z(T) * Cp \quad \textbf{(module 2)}$$

where: Cp is a constant for predation = $Cp_{Tbase} * e^{-fz(T)*Tbase}$
Cp_{Tbase} = predation at *Tbase*
Tbase = base temperature

$$zp_{Z\text{-}out} = \frac{Zi^2 f_z(T) * Cp}{K_P + Zi} \quad \textbf{(module 3)}$$

where: K_P is a half-saturation constant for predator grazing

ni: nitrification (27)

from NH_4 to NO_3, from O_2 to NO_3

$$ni_{NH4\text{-}NO3} = [ni_{max}/(K_{ni} + NH_4)] * NH_4 * e^{-(Ca*E)} * \frac{O_2}{K_{ni\,O2} + O_2}$$

where: ni_{max} = maximal rate for nitrification
K_{ni} = half saturation constant for nitrification of NH_4 to NO_3
K_{niO2} = half saturation constant for nitrification of NH_4 to O_2
Ca = is a dummy constant (exponential is to turn off in daylight;
product of *Ca** E should exceed 5 early on in day)
E = light (input)

$$ni_{O2\text{-}NO3} = ni_{NH4\text{-}NO3} / stoich(N:O)_1 \qquad [NH_3 + 2O_2 = HNO_3 + H_2O \text{ so } stoichN:O = 0.5]$$

br: bacterial respiration (28)

from O_2 to DOC, lPOC, RPOC

$$br_{O2\text{-}DOC} = bm_{DOC\text{-}CO2} / stoich(C:O)_4$$
$$br_{O2\text{-}lPOC} = bm_{lPOC\text{-}CO2} / stoich(C:O)_5$$
$$br_{O2\text{-}RPOC} = bm_{RPOC\text{-}CO2} / stoich(C:O)_5$$

bm: bacterial remineralization (25a,b, 26a,b, 30)

from lPOM to NH_4, PO_4, from DOM to NH_4, PO_4 , from rPOM to NH_4, PO_4

$$bm_{lPOC\text{-}CO2} = Cb * lPOC * \frac{O_2}{K_{b\,O2} + O_2}$$

where: *Cb* is a constant for remineralization of labile pool
$K_{b\,O2}$ is a half saturation constant for remineralization of O_2

$bm_{lPON\text{-}NH4} = bm_{lPOC\text{-}CO2}$ / stoich(C:N)$_{17}$
$bm_{lPOP\text{-}\text{-}PO4} = bm_{lPOC\text{-}CO2}$ / stoich(C:P)$_{16}$

$$bm_{DOC\text{-}CO2} = Cc * DOC * \frac{O_2}{K_{b\,O2} + O_2}$$

where: *Cc* is a constant for remineralization of DOM
$K_{b\,O2}$ is a half saturation constant for remineralization of O_2

$bm_{DON\text{-}NH4} = bm_{DOC\text{-}CO2}$ / stoich(C:N)$_{18}$
$bm_{DOP\text{-}PO4} = bm_{DOC\text{-}CO2}$ / stoich(C:P)$_{17}$

$$bm_{rPOC\text{-}CO2} = Cg * rPOC * \frac{O_2}{K_{b\,O2} + O_2}$$

where: *Cg* is a constant for slow refractory remineralization
$K_{b\,O2}$ is a half saturation constant for remineralization of O_2

$bm_{rPON\text{-}NH4} = bm_{rPOC\text{-}CO2}$ / stoich(C:N)$_{19}$
$bm_{rPOP\text{-}PO4} = bm_{rPOC\text{-}CO2}$ / stoich(C:P)$_{18}$

so: solublization/bacterial degradation (29)

from lPOM to DOM

$so_{lPOC\text{-}DOC} = Cs * lPOC$ *where:* *Cs* is a constant for solubilization
$so_{lPON\text{-}DON} = so_{DOC}$ / stoich(C:N)$_{20}$
$so_{lPOP\text{-}DOP} = so_{DOC}$ / stoich(C:P)$_{19}$

ds: detrital sinking (23)

from lPOM, rPOM to out

$ds_{lPOM\text{-}out} = -d/dz\ (w_{detl} * lPOM)$
where: w_{det} = a depth-varying sinking rate for labile detritus
$ds_{rPOM\text{-}out} = -d/dz\ (w_{detr} * rPOM)$
where: w_{detr} = a depth-varying sinking rate for refractory detritus

and where: eqns for lPOC and rPOC are as written
eqns for lPON have "/stoich(C:N)$_{15}$" and rPON have "/stoich(C:N)$_{16}$"
eqns for lPOP have "/stoich(C:P)$_{14}$" and rPOP have "/stoich(C:P)$_{15}$"

Constants and coefficients:

Ri = temperature growth coefficient for Pi
E_ki = light saturation coefficient for Pi
μ_oi = maximal growth rate for Pi
μ_oi_{Tbase} = maximal growth rate for Pi at *Tbase*
I_{max} = maximal ingestion rate of prey (currently assuming constant for all prey types)
$I_{maxTbase}$ = maximal ingestion rate of prey at *Tbase*
ni_{max} = maximal rate for nitrification of NH_4 to NO_3
ϕj = preference for prey type, j=1-8:1=P1,2=P2,3=P3,4=Z1, 5=Z2, 6=Z3, 7=lPOM, 8=rPOM
K_{iA} = half-saturation constant for total food
K_{iO2} = half saturation constant for Zi on O_2
K_i[nutr] = half saturation constant for Pi on nutrient [NO_3, NH_4, PO_4]
$K_{b\,O2}$ = half saturation constant for remineralization of O_2
K_P = half-saturation constant for predator grazing on Zi
K_{ni} = half saturation constant for nitrification of NH_4 to NO_3
K_{niO2} = half saturation constant for nitrification of NH_4 to O_2
Ca is a dummy constant (exponential is to turn off in daylight)
Cb is a constant for remineralization of labile pool
Cc is a constant for remineralization of DOM
Cd is a constant for zooplankton exudation
Cd_{Tbase} is a constant for zooplankton exudation at *Tbase*
Ce is a constant for zooplankton egestion to labile pool
Ce_{Tbase} is a constant for zooplankton egestion to labile pool at *Tbase*
Cf is a constant for zooplankton egestion to refractory pool
Cf_{Tbase} is a constant for zooplankton egestion to refractory pool at *Tbase*
Cg is a constant for slow refractory remineralization
Ch is a constant for basal metabolism
Ch_{Tbase} is a constant for basal metabolism at *Tbase*
Cl is a constant for phytoplankton death to labile pool
Cm is a constant for zooplankton death to labile pool
Cm_{Tbase} is a constant for zooplankton death to labile pool at *Tbase*
Cn is a constant for zooplankton death to refractory pool
Cn_{Tbase} is a constant for zooplankton death to refractory pool at *Tbase*
Co is a feeding threshold level, below which no grazing occurs
Cp is a constant for predation
Cp_{Tbase} is a constant predation at *Tbase*
Cq is a constant for phytoplankton respiration
Cr is a constant for phytoplankton death to refractory pool
Cs is a constant for phytoplankton solubilization
Cx is a constant for phytoplankton exudation
Cz is a constant for zooplankton respiration
Cz_{Tbase} is a constant for zooplankton respiration at *Tbase*
w_{det} = a depth-varying sinking rate for detritus
w_{zoo} = a depth-varying movement rate for zooplankton
w_{phy} = a depth-varying sinking rate for phytoplankton
$f_z(T)$ is a temperature coefficient
Tbase is a base temperature

Calculated variables:

A = total food available
rnu_{NH4} = preferential uptake for ammonium
rnu_{NO3} = preferential uptake for nitrate

Input variables:
T = temperature
E = light

Stoichiometries*:*

Assume stoich C:N of P*i* =6, Z*i* =4, DOM=calculated, labile POM =calculated, refractory POM=calculated; stoich C:P of P*i* =96, Z*i* =64, DOM=calculated, labile POM =calculated, refractory POM=calculated.

stoich(C:N)$_1$ for CO_2:NO_3 uptake = [stoich(C:N) P*i=6*]
stoich(C:N)$_2$ for CO_2:NH_4 uptake = [stoich(C:N) P*i=6*]
stoich(C:N)$_3$ for CO_2:NH_4 excretion from phytoplankton = [stoich(C:N) P*i=6*]
stoich(C:N)$_4$ for DOC:DON exudation from phytoplankton = [stoich(C:N) P*i=6*]
stoich(C:N)$_5$ for labile POC:PON from phytoplankton death = [stoich(C:N) P*i=6*]
stoich(C:N)$_6$ for refractory POC:PON from phytoplankton death = [stoich(C:N) P*i=6*]
stoich(C:N)$_7$ for CO_2:NH_4 excretion from zooplankton [=3.5]
stoich(C:N)$_8$ for labile pool POC:PON grazed by zooplankton [= calculated]
stoich(C:N)$_9$ for refractory pool POC:PON grazed by zooplankton [= calculated]
stoich(C:N)$_{10}$ for DOC:DON exuded by zooplankton [=15]
stoich(C:N)$_{11}$ for labile POC:PON from zooplankton mortality = [stoich(C:N) Z*i=4*]
stoich(C:N)$_{12}$ for refractory POC:PON from zooplankton mortality = [stoich(C:N) Z*i=4*]
stoich(C:N)$_{13}$ for labile POC:PON egested by zooplankton [= calculated]
stoich(C:N)$_{14}$ for refractory POC:PON egested by zooplankton [= calculated]
stoich(C:N)$_{15}$ for sinking labile pool POC:PON [= calculated]
stoich(C:N)$_{16}$ for sinking refractory pool POC:PON [= calculated]
stoich(C:N)$_{17}$ for labile POC:PON remineralized to NH_4 [= calculated or constant]
stoich(C:N)$_{18}$ for DOC:DON remineralized to NH_4 [= calculated or constant]
stoich(C:N)$_{19}$ for refractory POC:PON remineralized to NH_4 [= calculated or constant]
stoich(C:N)$_{20}$ for labile POC:PON solubized to DOM [= calculated or constant]

stoich(C:P)$_1$ for CO_2:PO_4 uptake = [stoich(C:P) P*i=96*]
stoich(C:P)$_2$ for CO_2:PO_4 excretion from phytoplankton = [stoich(C:P) P*i=96*]
stoich(C:P)$_3$ for DOC:DOP exudation from phytoplankton = [stoich(C:P) P*i=96*]
stoich(C:P)$_4$ for labile POC:POP from phytoplankton death = [stoich(C:P) P*i=96*]
stoich(C:P)$_5$ for refractory POC:POP from phytoplankton death = [stoich(C:P) P*i=96*]
stoich(C:P)$_6$ for CO_2:PO_4 excretion from zooplankton [= 56]
stoich(C:P)$_7$ labile pool POC:POP grazed by zooplankton [= calculated]
stoich(C:P)$_8$ for refractory pool POC:POP grazed by zooplankton [= calculated]
stoich(C:P)$_9$ for DOC:DOP exuded by zooplankton [= *240*]
stoich(C:P)$_{10}$ for labile POC:POP from zooplankton mortality = [stoich(C:P) Z*i=64*]
stoich(C:P)$_{11}$ for refractory POC:POP from zooplankton mortality = [stoich(C:P) Z*i=64*]
stoich(C:P)$_{12}$ for labile POC:POP egested by zooplankton [= calculated]
stoich(C:P)$_{13}$ for refractory POC:POP egested by zooplankton [= calculated]
stoich(C:P)$_{14}$ for sinking labile pool POC:PON [= calculated]
stoich(C:P)$_{15}$ for sinking refractory pool POC:PON [= calculated]
stoich(C:P)$_{16}$ for labile POC:POP remineralized to PO_4 [= calculated or constant]
stoich(C:P)$_{17}$ for DOC:DOP remineralized to PO_4 [= calculated or constant]
stoich(C:P)$_{18}$ for refractory POC:POP remineralized to PO_4 [= calculated or constant]
stoich(C:P)$_{19}$ for labile POC:POP solubized to DOM [= calculated or constant]

stoich(C:O)$_1$ for CO_2:O_2 of photosynthesis = [stoich(C:O)*all=1*]
stoich(C:O)$_2$ for CO_2:O_2 of phytoplankton respiration = [stoich(C:O)*all=1*]
stoich(C:O)$_3$ for CO_2:O_2 of zooplankton respiration = [stoich(C:O)*all =1*]
stoich(C:O)$_4$ for CO_2:O_2 of bacterial respiration of DOC = [stoich(C:O)*all =1*]
stoich(C:O)$_5$ for CO_2:O_2 of bacterial respiration of labile POC = [stoich(C:O)*all=1*]

stoich(N:O)$_1$ for NH_4:O2 during nitrification [=0.5]

PHYTOPLANKTON:

ps: photosynthesis

ps $_{\text{P-O2}}$

ne: nutrient excretion from phytoplankton

ne $_{\text{P-NH4}}$
ne $_{\text{P-PO4}}$

pd: phytoplankton death

pd $_{\text{P-lPOC}}$
pd $_{\text{P-lPON}}$
pd $_{\text{P-lPOP}}$
pd $_{\text{P-rPOC}}$
pd $_{\text{P-rPON}}$
pd $_{\text{P-rPOP}}$

pe: phytoplankton exudation

pe $_{\text{P-DOC}}$
pe $_{\text{P-DON}}$
pe $_{\text{P-DOP}}$

cs: cell sinking

cs $_{\text{P-out}}$

pr: phytoplankton respiration

pr $_{\text{O2-P}}$

nu: nutrient uptake

nu $_{\text{NO3-P}}$
nu $_{\text{NH4-P}}$
nu $_{\text{PO4-P}}$

ZOOPLANKTON:

nx: nutrient excretion from zooplankton

nx $_{\text{Z-NH4}}$
nx $_{\text{Z-PO4}}$

zd: zooplankton exudation

zd $_{\text{Z-DOC}}$
zd $_{\text{Z-DON}}$
zd $_{\text{Z-DOP}}$

ze: zooplankgon egestion

ze $_{\text{Z-lPOC}}$
ze $_{\text{Z-lPON}}$
ze $_{\text{Z-lPOP}}$
ze $_{\text{Z-rPOC}}$
ze $_{\text{Z-rPON}}$
ze $_{\text{Z-rPOP}}$

zm: zooplankton mortality

zm $_{\text{Z-Lpoc}}$
zm $_{\text{Z-lPON}}$
zm $_{\text{Z-lPOP}}$
zm $_{\text{Z-rPOC}}$
zm $_{\text{Z-rPON}}$
zm $_{\text{Z-rPOP}}$

zp: predation on zooplankton

zp $_{\text{Z-out}}$

zg: zooplankton grazing

zg = dg + cg + hg

hg: herbivorous grazing

hg $_{\text{P-Z}}$

cg: carnivorous grazing

cg $_{\text{Z-Z}}$

dg: detrital grazing

dg $_{\text{lPOC-Z}}$
dg $_{\text{lPON-Z}}$
dg $_{\text{lPOP-Z}}$
dg $_{\text{rPOC-Z}}$
dg $_{\text{rPON-Z}}$
dg $_{\text{rPOP-Z}}$

zr: zooplankton respiration

zr $_{\text{O2-Z}}$

zs: zooplankton swimming

zs $_{\text{Z-Z}}$

BACTERIAL PROCESSES:

ni: nitrification

$\text{ni}_{\text{NH4-NO3}}$
$\text{ni}_{\text{O2-NO3}}$

br: bacterial respiration

$\text{br}_{\text{O2-DOC}}$
$\text{br}_{\text{O2-lPOC}}$
$\text{br}_{\text{O2-RPOC}}$

bm: bacterial remineralization

$\text{bm}_{\text{lPOC-CO2}}$
$\text{bm}_{\text{lPON-NH4}}$
$\text{bm}_{\text{lPOP--PO4}}$
$\text{bm}_{\text{DOC-CO2}}$
$\text{bm}_{\text{DON-NH4}}$
$\text{bm}_{\text{DOP-PO4}}$
$\text{bm}_{\text{rPOC-CO2}}$
$\text{bm}_{\text{rPON-NH4}}$
$\text{bm}_{\text{rPOP-PO4}}$

so: solublization/bacterial degradation

$\text{so}_{\text{lPOC-DOC}}$
$\text{so}_{\text{lPON-DON}}$
$\text{so}_{\text{lPOP-DOP}}$

DETRITUS:

ds: detrital sinking

$\text{ds}_{\text{lPOC-out}}$
$\text{ds}_{\text{lPON-out}}$
$\text{ds}_{\text{lPOP-out}}$
$\text{ds}_{\text{rPOC-out}}$
$\text{ds}_{\text{rPON-out}}$
$\text{ds}_{\text{rPOP-out}}$

ALPHABETICAL TRANSFER PROCESS NAMES

bm: bacterial remineralization (25a,b, 26a,b, 30)
from lPOM to NH_4, PO_4, *from DOM to* NH_4, PO_4 , *from rPOM to* NH_4, PO_4

br: bacterial respiration (28)
from O_2 *to DOC, lPOC*

cg: carnivorous grazing (10-12)
from Zi to Zi; i = 1-3

cs: cell sinking (24)
from Pi to out

dg: detrital grazing (21a, b)
from lPOM, rPOM to Zi

ds: detrital sinking (23)
from lPOM, rPOM to out

hg: herbivorous grazing (1-9)
from Pi to Zi; i = 1-3

ne: nutrient excretion from phytoplankton (14a, b)
from Pi to NH_4, PO_4

ni: nitrification (27)
from NH_4 *to* NO_3, *from* O_2 *to* NO_3

nx: nutrient excretion from zooplankton (19a, b)
from Zi to NH_4, PO_4

nu: nutrient uptake (13a, b, c)
from NO_3, NH_4, PO_4 *to Pi*

pd: phytoplankton death (15b, c)
from Pi to (lPOM+rPOM)

pe: phytoplankton exudation (15a)
from Pi to DOM

pr: phytoplankton respiration (17)
from O_2 *to Pi*

ps: photosynthesis (16)
from Pi to O_2

so: solublization/bacterial degradation (29)
from lPOM to DOM

zd: zooplankton exudation (22a)
from Zi to DOM

ze: zooplankgon egestion (22d, e)
from Zi to (lPOM + rPOM)

zg: zooplankton grazing (1-12, 21a,b)
from (lPOM + rPOM + Pi + Zi) to Zi

zm: zooplankton mortality (22b, c)
from Zi to (lPOM + rPOM)

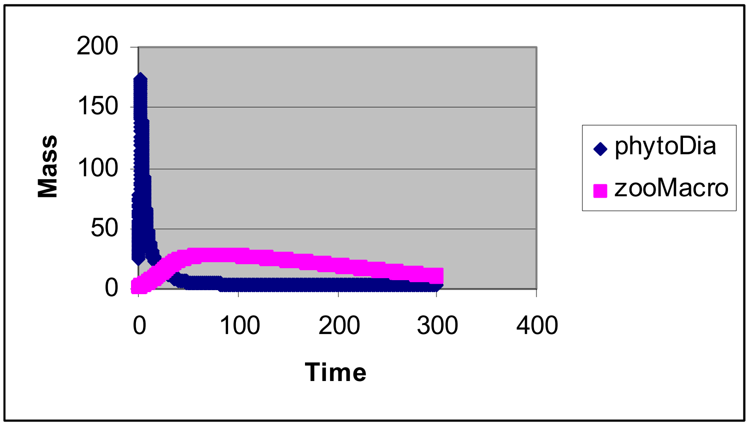
zp: predation on zooplankton (20)
from Zi to out

zr: zooplankton respiration (18)
from O_2 *to Zi*

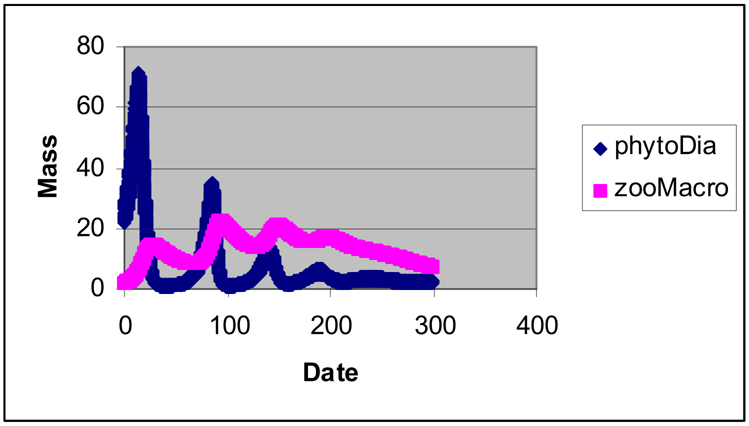
zs: zooplankton swimming
within any Zi, among depth boxes

Appendix B: Sample Outputs

Growth of Phytoplankton and Zooplankton with Constant Light



Growth of Phytoplankton and Zooplankton with Non-Constant Light



Appendix C: Scheduler