The Biological Model Equations

The biological model consists of nine compartments describing small phytoplankton (*S1*), diatoms (*S2*), microzooplankton (*Z1*), mesozooplankton (*Z2*), nonliving particulate organic nitrogen (*DN*), nonliving particulate organic silicate (*DSI)*, dissolved silicate ($Si(OH)_4$), and two forms of dissolved inorganic nitrogen: nitrate (NO_3) and ammonium (NH_4). Figure 1 depicts the inter-compartment flows of the ecosystem. Nine equations describing each compartment all take the form:

Eq. 1

$$\frac{\partial C_i}{\partial t} = PHYSICS(C_i) + BIOLOGY(C_i) \qquad i = 1,......,9$$

(For example, $C_1=NO_3$, $C_2=NH_4$, and so on). The term $PHYSICS(C_i)$ represents the contribution to the concentration change due to physical processes, including vertical advection and eddy diffusion.

Eq. 2

$$PHYSICS(C_i) = \underbrace{-w\frac{\partial C_i}{\partial z}}_{advection} \underbrace{+\frac{\partial}{\partial z}\left(A_{Tv}\frac{\partial C_i}{\partial z}\right)}_{eddy\ \ diffusivity}$$

Here w is vertical velocity, and A_{Tv} is vertical eddy diffusion coefficient. The values for w and A_{Tv} are the area-averaged over 5°S-5°N and 90°W-180° (the Wyrtki Box) annual mean upwelling velocity and vertical eddy diffusion, which are obtained from the simulations of the three-dimensional ocean circulation model in the region (see Chai et al. 1997 for details). The term $BIOLOGY(C_i)$ represents biological sources and sinks of that compartment. All parameters used in the calculation of $BIOLOGY(C_i)$ are defined in Table 1. In the euphotic zone (the upper 120 m), the biological terms, $BIOLOGY(C_i)$, are:

Eq. 3 $$BIOLOGY(NO_3) = \underbrace{-NPS1}_{NO_3\ update\ by\ S1}\ \underbrace{-(NPS2 - RPS2)}_{NO_3\ update\ by\ S2}$$

Eq. 4 $$BIOLOGY(Si(OH)_4) = \underbrace{-NPS2}_{Si(OH)_4\ update\ by\ S2}$$

Eq. 5 $$BIOLOGY(NH_4) = \underbrace{-RPS1}_{NH_4\ update\ by\ S1}\ \underbrace{-RPS2}_{NH_4\ update\ by\ S2}\ \underbrace{+reg_1 Z1 + reg_2 Z2}_{NH_4\ regeneration\ by\ Z1\ and\ Z2}$$

reg_1 = 0.2 day^{-1} (microzooplankton excretion rate to ammonium)
reg_2 = 0.1 day^{-1} (mesozooplankton excretion rate to ammonium)

Eq. 6 $$BIOLOGY(S1) = \underbrace{(NPS1 + RPS1)}_{total\ production\ by\ S1}\ \underbrace{-G_1}_{grazing\ by\ Z1}$$

Eq. 7 $$BIOLOGY(S2) = \underbrace{2NPS2}_{production\ by\ S2}\ \underbrace{-2G_2}_{grazing\ by\ S2}\ \underbrace{-2\partial(w_1 S2)/\partial z}_{S2\ sinking}$$

w_1 = 1.0 m day^{-1} (diatoms sinking speed)
Note: all the source and sink terms are counted twice here in order to reflect both nitrogen and silicate uptake by diatoms, nitrogen to silicate ratio is 1 to 1 in diatoms.

Eq. 8 $$BIOLOGY(Z1) = \underbrace{G_1}_{grazing\ on\ S1}\ \underbrace{-G_3}_{predation\ by\ Z2}\ \underbrace{-reg_1\ Z1}_{NH_4\ regeneration}$$

Eq. 9 $$BIOLOGY(Z2) = \underbrace{(G_2 + G_3 + G_4)}_{total\ grazing\ by\ Z2}\ \underbrace{-(1-\gamma_1)(G_2 + G_3 + G_4)}_{detritus-N\ prod.\ from\ Z2}\ \underbrace{-reg_2\ Z2}_{NH_4\ reg.}\ \underbrace{-\gamma_2 Z2^2}_{loss}$$

$\gamma_1 = 0.75$ (mesozooplankton assimilation efficiency)
$\gamma_2 = 0.05$ $(mmol\ m^{-3})^{-1}\ day^{-1}$ (mesozooplankton specific mortality rate)
Note: the fecal pellet production of silicate by Z2 equals to the grazing on diatoms by Z2, which is G_2, two terms cancel each other in the equation (9). In the sense, the Z2 component just passes the silicate from the diatoms directly to the detritus-Si pool.

Eq. 10 $$BIOLOGY(DN) = \underbrace{(1-\gamma_1)(G_2 + G_3 + G_4)}_{detritus\text{-}N\ prod.\ by\ Z2}\ \underbrace{-G_4}_{grazing\ by\ Z2}\ \underbrace{-\partial(w_2 DN)/\partial z}_{sinking}$$

w_2 = 10.0 m day^{-1} (detritus sinking speed)

Eq. 11 $$BIOLOGY(DSI) = \underbrace{G_2}_{detritus\text{-}Si\ prod.}\ \underbrace{-\partial(w_2 DSI)/\partial z}_{sinking}$$

Growth and grazing functions can be written as follows:

Eq. 12 $$NPS1 = \mu 1_{max}\ \underbrace{NO_3/(K_{NO_3} + NO_3)}_{NO_3\ regulation}\ \underbrace{e^{-\psi NH_4}}_{NH_4\ inhibition}\ \underbrace{\left(1 - e^{-\alpha I/\mu 1_{max}}\right)}_{light\ regulation}\ S1$$

$\mu 1_{max}$ = 2.0 day^{-1} (maximum specific growth rate of small phytoplankton)
ψ = 5.59 (mmol m^{-3})$^{-1}$ (ammonium inhibition parameter)
K_{no3} = 0.5 mmol m^{-3} (half-saturation for nitrate uptake by S1)
α = 0.025 (W m^{-2})$^{-1}$ day^{-1} (initial slope of P-I curve)

I is the irradiance, and is given by:

Eq. 13 $$I(z,\ t) = I_o(t)\ e^{-k_1 z\ -k_2 \int_{-z}^{0} (S1+S2)\ dz}$$

k_1 = 0.046 m^{-1} (light attenuation due to water)
k_2 = 0.03 m^{-1} (light attenuation by small phytoplankton and diatoms)

$I_o(t)$ is the surface irradiance, and during a 24 hour period, takes the form:

Eq. 14 $$I_o(t) = \begin{cases} I_o^{Noon}\ \sin\left(\dfrac{t-6}{12}\pi\right) & (\textit{from } 6 \textit{ am to } 6 \textit{ pm}) \\ 0 & (\textit{from } 6 \textit{ pm to } 6 \textit{ am}) \end{cases}$$

I_o^{Noon} = 410 W m^{-2} (annual averaged noontime averaged surface irradiance)

Eq. 15 $$RPS1 = \mu 1_{max}\ \underbrace{NH_4/(K_{NH_4} + NH_4)}_{NH_4\ regulation}\ \underbrace{\left(1 - e^{-\alpha I/\mu 1_{max}}\right)}_{light\ regulation}\ S1$$

K_{NH4} = 0.05 mmol m^{-3} (half-saturation for ammonium uptake by S1)

Eq. 16 $$NPS2 = \mu 2_{max}\ \underbrace{Si(OH)_4/(K_{Si(OH)_4} + Si(OH)_4)}_{Si(OH)_4\ regulation}\ \underbrace{\left(1 - e^{-\alpha I/\mu 1_{max}}\right)}_{light\ regulation}\ S2$$

$\mu 2_{max}$ = 1.5 day^{-1} (maximum specific growth rate of diatoms)
$K_{Si(OH)4}$ = 3.0 mmol m^{-3} (half-saturation for $Si(OH)_4$ uptake by *S2*)

Eq. 17 $$RPS2 = \mu 2_{max}\ \underbrace{NH_4/(K_{S2-NH_4} + NH_4)}_{NH_4\ regulation}\ \underbrace{\left(1 - e^{-\alpha I/\mu 1_{max}}\right)}_{light\ regulation}\ S2$$

K_{S2-NH4} = 1.0 mmol m^{-3} (Half-saturation for ammonium uptake by diatoms)

Eq. 18 $$G_1 = G1_{max}\ \underbrace{S1/(K1_{gr} + S1)}_{food\ regulation}\ \underbrace{S1/S1_{ave}}_{depth\ modification}\ Z1$$

$G1_{max}$ = 1.25 day^{-1} (microzooplankton maximum growth rate)
$K1_{gr}$ = 0.5 mmol m^{-3} (half-saturation for micro zooplankton ingestion)

$S1_{ave}$ is depth averaged (within the euphotic zone) small phytoplankton, which is defined as:

Eq. 19 $$S1_{ave} = \frac{1}{z'} \int_{-z'}^{0} S1\ dz$$

I found that the predator-prey oscillation could be reduced significantly in the model by modifying the grazing functions with terms $S1/S1_{ave}$. The z' is the depth of euphotic zone, and is set to 120 m in the model.

Eq. 20 $$G_2 = G2_{max} \frac{\zeta_1 S2}{K2_{gr} + \zeta_1 S2 + \zeta_2 Z1 + \zeta_3 DN} Z2$$

Eq. 21 $$G_3 = G2_{max} \frac{\zeta_2 Z1}{K2_{gr} + \zeta_1 S2 + \zeta_2 Z1 + \zeta_3 DN} Z2$$

Eq. 22 $$G_4 = G2_{max} \frac{\zeta_3 DN}{K2_{gr} + \zeta_1 S2 + \zeta_2 Z1 + \zeta_3 DN} Z2$$

$G2_{max}$ = 0.5 day^{-1} (mesozooplankton maximum growth rate)
$K2_{gr}$ = 0.25 mmol m^{-3} (half-saturation for mesozooplankton ingestion)

ζ_1, ζ_2, and ζ_3 are the preferences for a given food type, and defined as following:

$$\zeta_1 = \frac{\rho_1 S1}{\rho_1 S1 + \rho_2 Z1 + \rho_3 DN}$$

Eq. 23 $$\zeta_2 = \frac{\rho_2 Z1}{\rho_1 S1 + \rho_2 Z1 + \rho_3 DN}$$

$$\zeta_3 = \frac{\rho_3 DN}{\rho_1 S1 + \rho_2 Z1 + \rho_3 DN}$$

$\rho_1 = 0.7$, $\rho_2 = 0.2$, $\rho_3 = 0.1$

Values of the parameters used in the standard experiment are given in Table 1. Selection of the parameters is primarily based upon four major sources: 1) papers by Fasham *et al*. (1990), Sarmiento *et al*. (1993), and Chai et al. (1996); 2) observational data in the equatorial Pacific (Dugdale and Goering, 1967; Dugdale *et al.* 1991; Barber and Chavez, 1991; Minas *et al.* 1986; Peña *et al.* 1991); 3) data from the 1992 EqPac cruises (Barber *et al*. 1995; Lindley *et al*. 1995; Landry *et al*. 1995; Murray *et al*. 1994); and 4) historical literature. The sources of the parameters are also given in Table 1.