

# Biological level model

## Equations

The Hood *et al.* (2000) six-compartment ecosystem model includes state variables representing dissolved inorganic nitrogen (*DIN*), dissolved organic nitrogen (*DON*), phytoplankton (*P*), *Trichodesmium* (*T*), detritus (*D*) and heterotrophs (*H*). The mass in each of these compartments is expressed in nitrogen concentration units (mmolesN/m<sup>3</sup>) and the model parameters are listed in biodat.f.

The *H* compartment is considered to represent the sum of all heterotrophic processes including, for example, bacteria, microzooplankton and mesozooplankton. Changes in *H* due to biological processes are determined as follows:

$$\begin{aligned} \frac{\partial H}{\partial t} = & ge_P h_P H C_m P + ge_D h_D H C_m D + (ge_H - 1) h_H C_m H^2 \\ & + ge_T h_T H C_m T + ge_{DON} h_{DON} H C_m DON \end{aligned} \quad (1)$$

Where the coefficients  $ge_i$  are heterotrophic growth efficiencies, for growth on phytoplankton ( $i = P$ ), *Trichodesmium* ( $i = T$ ), detritus ( $i = D$ ), *DON* ( $i = DON$ ) and other heterotrophs ( $i = H$ ). The coefficient  $C_m$  is the maximum heterotrophic consumption rate. In (1)

$$\begin{aligned} h_P &= \Phi_P / \Theta, \\ h_D &= \Phi_D / \Theta, \\ h_H &= \Phi_H / \Theta, \\ h_T &= \Phi_T / \Theta, \\ h_{DON} &= \Phi_{DON} / \Theta \end{aligned}$$

and

$$\Theta = \Phi_P P + \Phi_D D + \Phi_H H + \Phi_T T + \Phi_{DON} DON + HKS,$$

which allows assignment of “preferences” for the different forms of organic nitrogen. For simplicity, the half-saturation constant, *HKS*, is assumed to be the same for all substrates.

The *DIN* compartment is considered to represent the sum of all dissolved inorganic forms of nitrogen, *i.e.*, NO<sub>3</sub>, NO<sub>2</sub>, and NH<sub>4</sub><sup>+</sup>. Changes in *DIN*, due to biological processes are determined as follows

$$\begin{aligned} \frac{\partial DIN}{\partial t} = & \gamma(ae_P - ge_P) h_P H C_m P + \gamma(ae_D - ge_D) h_D H C_m D \\ & + \gamma(ae_H - ge_H) h_H H C_m H + \gamma(ae_T - ge_T) h_T H C_m T \\ & + (ae_{DON} - ge_{DON}) h_{DON} H C_m DON - U_P P - U_T T, \end{aligned} \quad (2)$$

where the positive terms represent heterotrophic remineralization of particulate and dissolved organic nitrogen to dissolved inorganic nitrogen, and the negative terms represent uptake of *DIN* by phytoplankton and *Trichodesmium*. The coefficients  $ae_i$  are assimilation efficiencies for heterotrophic growth on phytoplankton ( $i = P$ ), *Trichodesmium* ( $i = T$ ), detritus ( $i = D$ ), *DON* ( $i = DON$ ) and other heterotrophs ( $i = H$ ). The coefficient  $\gamma$  specifies the

fraction of remineralization that goes directly to *DIN*. Note that all of the *DON* consumed by heterotrophs (presumably bacteria) that is not assimilated is remineralized directly to *DIN*. In (2),

$$U_P = \mu_P(1 - e^{-I/I_P})e^{-I/I_{\beta P}} \frac{DIN}{DIN + PKS} \quad (3)$$

and

$$U_T = \mu_T(1 - e^{-I/I_T})e^{-I/I_{\beta T}} \frac{DIN}{DIN + TKS}, \quad (4)$$

which describe light and *DIN*-dependent variations in phytoplankton and *Trichodesmium* *DIN* uptake. An exponential saturation function with photoinhibition is used to describe the light dependence, and a Michaelis-Menten hyperbolic saturation function is used to describe the *N*-dependence. In (3) and (4),  $\mu_P$  and  $\mu_T$  are the maximum growth rates,  $I_P$  and  $I_T$  are light saturation parameters, and  $I_{\beta P}$  and  $I_{\beta T}$  are photoinhibition parameters for phytoplankton and *Trichodesmium*, respectively. The variable  $I$  is the subsurface irradiance. In addition, in (3) and (4),  $PKS$  and  $TKS$  are half saturation constants for *DIN* uptake for phytoplankton and *Trichodesmium*. Thus *Trichodesmium* spp. take up *DIN* following Michaelis-Menten kinetics. Finally, it is assumed here that direct heterotrophic utilization of *DIN* is negligible.

The growth equations for phytoplankton and trichodesmium are:

$$\frac{\partial P}{\partial t} = \alpha U_P P - S_P P - h_P HC_m P \quad (5)$$

and

$$\frac{\partial T}{\partial t} = \alpha G_T T - S_T T - h_T HC_m T. \quad (6)$$

In (5) and (6), the first term represents growth, the second natural mortality and the third consumption by heterotrophs. The heterotrophic consumptive terms are defined above. Natural mortality is modeled using linear functions with mortality rates  $S_P$  and  $S_T$  for phytoplankton and *Trichodesmium*, respectively. Light and *DIN*-dependent phytoplankton growth in (5) is modeled using  $U_P$  as defined in (3), but *Trichodesmium* growth in (6) is modeled using:

$$G_T = \mu_T(1 - e^{I/I_T})e^{-I/I_{\beta T}}. \quad (7)$$

Thus, although *Trichodesmium* spp. take up *DIN* according to (4) their growth rate is not limited by *DIN* availability. Therefore, when *DIN* concentrations are very low, *Trichodesmium* growth is supported almost entirely by  $N_2$ -fixation, and when *DIN* concentrations increase  $N_2$ -fixation is throttled back. Note also that there is no representation of phosphorous limitation in this model either. *i.e.*, it is assumed that nitrogen fixation provides an infinite supply of nitrogen and that *Trichodesmium* is able to obtain or retain the phosphorous required to support growth that is controlled principally by the availability of light.

An additional dimensionless coefficient  $\alpha$  in (5) and (6) determines the fraction of photosynthesis that remains in particulate form with remainder  $(1 - \alpha)$  partitioned to *DON*.

Changes in *DON* concentration due to biological processes are modeled using an equation similar to (2)

$$\begin{aligned} \frac{\partial DON}{\partial t} = & (1 - \gamma)(ae_P - ge_P)h_P HC_m P + (1 - \gamma)(ae_D - ge_D)h_D HC_m D \\ & + (1 - \gamma)(ae_H - ge_H)h_H HC_m H + (1 - \gamma)(ae_T - ge_T)h_T HC_m T \\ & + (1 - \alpha)G_T T + (1 - \alpha)U_P P + (1 - \beta)S_P P + (1 - \beta)S_T T \\ & - Hh_{DON} C_m DON. \end{aligned} \quad (8)$$

Here the positive terms with  $1 - \gamma$  coefficients represent heterotrophic remineralization of particulate organic nitrogen to dissolved organic nitrogen, and the positive terms with  $1 - \alpha$  coefficients represent direct contributions to the *DON* pool due to exudation by phytoplankton and *Trichodesmium*. There are also two additional *DON* source terms with  $1 - \beta$  coefficients which represent contributions to the *DON* pool due to natural mortality of phytoplankton and *Trichodesmium*. The last term in (8) represents uptake of *DON* by heterotrophs such as bacteria and *DON*-consuming protists. It should be noted that *DON* in this model is consumed as readily as any other particulate organic constituent and should therefore be considered “labile”.

Finally, changes in detritus concentration due to biological processes are modeled as follows:

$$\begin{aligned} \frac{\partial D}{\partial t} = & (1 - ae_P)h_P HC_m P + (1 - ae_H)h_H HC_m H \\ & + (1 - ae_T)h_T HC_m T + (1 - ae_D)h_D HC_m D \\ & + (1 - ae_{DON})h_{DON} HC_m DON + \beta S_P P + \beta S_T T \\ & - h_D HC_m D, \end{aligned} \quad (9)$$

where the terms with coefficients  $(1 - ae_i)$  represent contributions to the detritus pool due to egestion by heterotrophs, and the terms with coefficients  $\beta$  represent contributions to the detritus pool due to natural mortality of phytoplankton and *Trichodesmium*. The only loss term in (9) represents consumption of detritus by heterotrophs. It should be noted that the egestion term in (9) due to *DON* consumption by heterotrophs is actually zero because the assimilation efficiency for *DON* is taken to be 1 (see biodat.f). i.e., it is assumed that there is no egestion associated with *DON* consumption.

The biological model is integrated numerically over time using a fourth-order Runge-Kutta scheme.

## Mixing, Diffusion, Advection, and Sinking

All of the compartments in the biological model are subjected to mixing, diffusion and vertical advection. Diffusion is applied uniformly throughout the model domain using  $K_w = 0.0001 \text{ m}^2/\text{s}$  as specified in biodat.f. Mixing and vertical advection are specified using time-varying output ( $h_1$  and  $w_{adv}$ , respectively) from the McCreary *et al.* (2000) model. The mixing is achieved by simply homogenizing all biological quantities down to  $h_1$  and vertical advection is implemented using a simple, centered, finite-difference, gradient form advection

scheme. The gradient form is used here to prevent accumulation or loss of mass due to convergence or divergence in 1-D. Vertical exchange also occurs via sinking of detritus. This is done using a vertical advection equation which is solved numerically using a flux form, upstream numerical scheme. The flux form is used here to allow for increases and decreases in detritus due to vertically varying sinking speeds.

The top boundary of the model is closed for all biological and chemical constituents and the bottom boundary of the model is closed for all constituents except *DIN* and *D*. Advective and diffusive fluxes of *DIN* across the bottom boundary are specified using a fixed, deep ocean *DIN* concentration of 20 mmol/m<sup>3</sup> (as in McCreary et al., 1996 and 2000). The sinking flux of detritus out of the bottom boundary is controlled by the sinking rate of detritus,  $w$ , and the detritus concentration calculated by the model immediately above the bottom.

## Light

Absorption of solar radiation is simulated using a double exponential decay equation:

$$I_Z = I_0 \left[ R e^{-k_1 Z} + (1 - R) e^{-k_2 Z} \right], \quad (10)$$

where  $I_Z$  and  $I_0$  are instantaneous surface and subsurface solar insolutions,  $R$  and  $(1 - R)$  are the long and shortwave components of the insolation, and  $k_1$  and  $k_2$  are the long and shortwave diffuse attenuation coefficients, respectively. To incorporate the effects of light absorption by phytoplankton we set

$$k_2 = k_x + k_p(P + T). \quad (11)$$

Here  $k_x$  is the diffuse attenuation coefficient for water and substances other than phytoplankton and *Trichodesmium* and  $k_p$  is the biomass-specific attenuation coefficient defined above. Thus, phytoplankton and *Trichodesmium* attenuate the shortwave radiation, but attenuation of longwave radiation is considered to be negligible compared to water.