

# Optimality-based plankton ecosystem model equations

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The optimality-based plankton ecosystem model comprises eight states, dissolved inorganic N and P (DIN, DIP), phytoplankton C, N, P, Chl ( $C_{\text{Phy}}$ ,  $N_{\text{Phy}}$ ,  $P_{\text{Phy}}$ , Chl), and microzooplankton compartments for dinoflagellates and ciliates ( $C_{\text{Dino}}$ ,  $C_{\text{Cil}}$ ). The rates of change are

$$\frac{d\text{DIN}}{dt} = -V_{\text{Phy}}^{\text{N}} + X_{\text{Dino}}^{\text{N}} + X_{\text{Cil}}^{\text{N}} \quad (1)$$

$$\frac{d\text{DIP}}{dt} = -V_{\text{Phy}}^{\text{P}} + X_{\text{Dino}}^{\text{P}} + X_{\text{Cil}}^{\text{P}} \quad (2)$$

$$\frac{dC_{\text{Phy}}}{dt} = V_{\text{Phy}}^{\text{C}} - I_{\text{Phy}}^{\text{C}} \quad (3)$$

$$\frac{dN_{\text{Phy}}}{dt} = V_{\text{Phy}}^{\text{N}} - I_{\text{Phy}}^{\text{C}} \cdot Q_{\text{Phy}}^{\text{N}} \quad (4)$$

$$\frac{dP_{\text{Phy}}}{dt} = V_{\text{Phy}}^{\text{P}} - I_{\text{Phy}}^{\text{C}} \cdot Q_{\text{Phy}}^{\text{P}} \quad (5)$$

$$\frac{d\text{Chl}}{dt} = \frac{dC_{\text{Phy}}}{dt} \cdot \theta + \frac{d\theta}{dt} \cdot C_{\text{Phy}} \quad (6)$$

$$\frac{dC_{\text{Dino}}}{dt} = V_{\text{Dino}}^{\text{C}} - I_{\text{Dino}}^{\text{C}} \quad (7)$$

$$\frac{dC_{\text{Cil}}}{dt} = V_{\text{Cil}}^{\text{C}} - I_{\text{Cil}}^{\text{C}} \quad (8)$$

where the superscripts denote the element (C, N, or P),  $V$  is assimilation into the state indicated by the subscript,  $I$  total ingestion by dinoflagellates and ciliates of the compartment in the subscript,  $X$  is excretion,  $R$  respiration,  $Q$  the cell quota (N:C or P:C ratio), and  $\theta$  the Chl: $C_{\text{Phy}}$  ratio.

The individual fluxes in the right-hand sides of (1)–(8) have been derived with the help of the optimality principle, assuming that phytoplankton and zooplankton allocate their intracellular resources among the competing requirements for resource acquisition and growth so as to maximise net relative growth rate (Pahlow et al. 2013; Pahlow & Prowe 2010).

## Phytoplankton

The optimality-based model of Pahlow et al. (2013) implements the chain-model concept that the maximal N uptake rate ( $V_{\text{max}}^{\text{N}}$ ) is a function of the phytoplankton P quota  $Q_{\text{Phy}}^{\text{P}}$ :

$$V_{\text{Phy}}^{\text{N}} = f_{\text{V}} f_{\text{N}} \widehat{V}^{\text{N}} \quad V_{\text{Phy}}^{\text{P}} = f_{\text{V}} (1 - f_{\text{N}}) \widehat{V}^{\text{P}} \quad (9)$$

where

$$\widehat{V}^{\text{N}} = \left( \sqrt{\frac{1}{V_{\text{max}}^{\text{N}}}} + \sqrt{\frac{1}{A_0 \text{DIN}}} \right)^{-2} \quad \widehat{V}^{\text{P}} = \left( \sqrt{\frac{1}{V_{\text{max}}^{\text{P}}}} + \sqrt{\frac{1}{A_0 \text{DIP}}} \right)^{-2} \quad (10)$$

$$V_{\max}^N = V_0 \left( 1 - \frac{Q_0^P}{Q_{\text{Phy}}^P} \right) \quad V_{\max}^P = V_0 \quad (11)$$

$$f_N = \frac{1}{1 + \sqrt{\frac{Q_0^P}{Q_{\text{Phy}}^N} \frac{V_0}{\widehat{V}^P} \left( \frac{\widehat{V}^N}{V_{\max}^N} \right)^{1.5}}} \quad (12)$$

$A_0$  is phytoplankton nutrient affinity,  $V_0$  the maximum-rate parameter, and  $Q_0^P$  the phosphorus subsistence quota for phytoplankton.

$$V_{\text{Phy}}^C = \left( 1 - \frac{1}{2} \frac{Q_0^N}{Q_{\text{Phy}}^N} - f_V \right) \mathcal{A} - f_V \zeta^N V_{\text{Phy}}^N - r_{\text{Phy}}^C \quad f_V = \frac{1}{2} \frac{Q_0^N}{Q_{\text{Phy}}^N} - \zeta^N (Q_{\text{Phy}}^N - Q_0^N) \quad (13)$$

where  $Q_0^N$  is the N subsistence quota (minimum N:C ratio),  $r_{\text{Phy}}^C$  transient C release (see below),  $f_V$  the allocation of cellular N towards nutrient acquisition,

$$\mathcal{A} = L_{\text{day}} V_0 \left( 1 - e^{-\frac{\alpha \hat{\theta} \text{PAR}}{V_0}} \right) (1 - \zeta^{\text{Chl}} \hat{\theta}) - R_M^{\text{Chl}} \zeta^{\text{Chl}} \hat{\theta} \quad \theta = \left( 1 - \frac{1}{2} \frac{Q_0^N}{Q_{\text{Phy}}^N} - f_V \right) \hat{\theta} \quad (14)$$

describes the light (PAR) dependence of photosynthesis,  $\hat{\theta}$  is the Chl:C ratio of the chloroplast,  $\alpha$  light affinity,  $\zeta^{\text{Chl}}$  the C requirement of the photosynthetic pigments (Chl),  $R_M^{\text{Chl}} = 0.1 \text{ d}^{-1}$  the cost of Chl maintenance, and  $L_{\text{day}}$  daylength as a fraction of 24 h. Since  $\mathcal{A}$  does not depend on  $Q_{\text{Phy}}^N$ , light harvesting can be regulated independently from nutrient acquisition.  $\hat{\theta}$  is a function of PAR so that  $\mathcal{A}$  is maximised, which is achieved by

$$\hat{\theta} = \begin{cases} \frac{1}{\zeta^{\text{Chl}}} + \frac{V_0}{\alpha \text{PAR}} \left\{ 1 - W_0 \left[ \left( 1 + \frac{R_M^{\text{Chl}}}{L_{\text{day}} V_0} \right) \exp \left( 1 + \frac{\alpha \text{PAR}}{V_0 \zeta^{\text{Chl}}} \right) \right] \right\} & \text{if } \text{PAR} > \text{PAR}_0 \\ 0 & \text{if } \text{PAR} \leq \text{PAR}_0 \end{cases} \quad (15)$$

where  $\text{PAR}_0 = \zeta^{\text{Chl}} R_M^{\text{Chl}} / (L_{\text{day}} \alpha)$  is the minimum light intensity allowing the algae to gain energy from light harvesting and  $W_0$  is the 0-branch of Lambert's W function (Barry et al. 2000). See Pahlow et al. (2013) for details.

In the chain model,  $Q_{\text{Phy}}^P$  has no direct effect on  $V_{\text{Phy}}^C$ . Hence, it is possible that  $Q_{\text{Phy}}^P < Q_0^P$  if P becomes temporarily limiting. In order to prevent  $Q_{\text{Phy}}^P < Q_0^P$ , we introduce a transient C release term,

$$r_{\text{Phy}}^C = \max \left[ V_{\text{Phy}}^C \frac{Q_0^P}{Q_{\text{Phy}}^P} - \frac{V_{\text{Phy}}^P}{Q_0^P}, 0 \right] \cdot \max \left( 2 - \frac{Q_{\text{Phy}}^P}{Q_0^P}, 0 \right) \quad (16)$$

releasing sufficient C but only when  $Q_{\text{Phy}}^P$  rapidly approaches  $Q_0^P$ .

## Zooplankton

The C:N:P stoichiometry of the phytoplankton compartment varies and is generally different from the (constant) composition of the dinoflagellates and ciliates. In order to maintain homeostasis, zooplankton thus excrete or egest some of the ingested material. This is implemented here with a cell-quota factor ( $f_Q$ ), defined as

$$f_Q = \min \left( \frac{Q_i^P}{Q_{\text{Zoo}}^P}, \frac{Q_i^N}{Q_{\text{Zoo}}^N}, 1 \right), \quad i \in [\text{Phy}, \text{Dino}, \text{Cil}] \quad (17)$$

where the subscript zoo refers to either Dino or Cil. Zooplankton net growth ( $V_{\text{zoo}}^{\text{C}}$ ) is the difference between assimilation and respiration costs of foraging, assimilation, and maintenance, corrected for the stoichiometric imbalance,

$$V_{\text{zoo}}^{\text{C}} = [EI^{\text{C}}(1 - c_a) - c_f A_{\text{F}} - R_{\text{M}}]f_{\text{Q}}, \quad E = E_{\text{max}} \left[ 1 - e^{-\beta \left( \frac{A_{\text{T}}}{A_{\text{F}}} - 1 \right)} \right] \quad (18)$$

where  $E$  is assimilation efficiency,  $c_a$  and  $c_f$  are the cost of assimilation and foraging coefficients, respectively,  $I^{\text{C}}$  total C ingestion,  $R_{\text{M}}$  maintenance respiration,  $E_{\text{max}} = 1$  maximum assimilation efficiency,  $\beta = 0.2$  the digestion coefficient, and  $A_{\text{T}}$  and  $A_{\text{F}}$  total and foraging activity, respectively. The subscript zoo here refers to either Dino or Cil in (7) and (8). Foraging activity and effective prey concentration,  $\Pi$ , determine  $I^{\text{C}}$ :

$$I^{\text{C}} = A_{\text{F}} \hat{I}, \quad \hat{I} = 1 - e^{-\Pi}, \quad \Pi = \sum_i \phi_i C_i, \quad i \in [\text{Phy}, \text{Dino}, \text{Cil}] \quad (19)$$

where  $\hat{I}$  is ingestion saturation,  $\phi_i$  and  $C_i$  are the prey capture coefficient and biomass concentration of prey type  $i$  (phytoplankton, dinoflagellates, or ciliates). Ingestion of individual prey types is then

$$I_i^{\text{C}} = \frac{\phi_i C_i}{\Pi} I^{\text{C}}, \quad i \in [\text{Phy}, \text{Dino}, \text{Cil}] \quad (20)$$

Foraging activity is a monotonically increasing function of  $\hat{I}$ :

$$A_{\text{F}} = \begin{cases} \frac{\beta A_{\text{T}}}{-1 - W_{-1} \left\{ - \left[ 1 - \frac{c_f}{E_{\text{max}} \hat{I} (1 - c_a)} \right] e^{-(1+\beta)} \right\}} & \text{if } \Pi > \Pi_{\text{th}} \\ 0 & \text{if } \Pi \leq \Pi_{\text{th}} \end{cases} \quad (21)$$

where  $\beta$  is the digestion coefficient,  $W_{-1}$  the  $-1$ -branch of Lambert's  $W$  function, and  $\Pi_{\text{th}}$  the effective feeding threshold, defined as

$$\Pi_{\text{th}} = \ln \frac{1}{1 - \frac{c_f}{E_{\text{max}}(1 - c_a)}} \quad (22)$$

Since  $A_{\text{T}}$  cannot be observed directly, it is more convenient to calculate  $A_{\text{T}}$  from the (observed) maximum ingestion rate  $I_{\text{max}}$ , which is obtained for  $\hat{I} = 1$ :

$$A_{\text{T}} = \frac{I_{\text{max}}}{\beta} \left\{ -1 - W_{-1} \left[ - \left( 1 - \frac{c_f}{E_{\text{max}}(1 - c_a)} \right) e^{-(1+\beta)} \right] \right\} \quad (23)$$

The release of N and P is obtained as the difference between ingestion and assimilation,

$$X_{\text{zoo}}^{\text{N}} = \sum_i I_i^{\text{C}} Q_i^{\text{N}} - V_{\text{zoo}}^{\text{C}} Q_{\text{zoo}}^{\text{N}}, \quad X_{\text{zoo}}^{\text{P}} = \sum_i I_i^{\text{C}} Q_i^{\text{P}} - V_{\text{zoo}}^{\text{C}} Q_{\text{zoo}}^{\text{P}}, \quad i \in [\text{Phy}, \text{Dino}, \text{Cil}] \quad (24)$$

See Pahlow & Prowe (2010) for the derivation of (18)–(23) and more details.

## References

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