

# Equations for OPPLA

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## 1 Functional types and state variables

The OPTimality-based PLAnkton ecosystem model (OPPLA) allows for up to 6 functional types, dissolved inorganic and organic matter, bacteria, phytoplankton, zooplankton, and detritus. Any number of bacterial, phytoplankton, and zooplankton groups can be specified for the ecosystem. Dissolved organic matter (DOM) comprises labile and refractory DOC and DON and labile DOP. Variable stoichiometry is implemented for phytoplankton and detritus. The rates of change of dissolved inorganic C, N, and P ( $C_i = \text{DIC}$ ,  $N_i = \text{DIN}$ ,  $P_i = \text{DIP}$ ), phytoplankton C, N, P, Chl ( $C_{\text{phy}}$ ,  $N_{\text{phy}}$ ,  $P_{\text{phy}}$ , Chl), and zooplankton compartments ( $C_{\text{zoo}}$ ) are

$$\frac{dY_i}{dt} = -V_{\text{phy}}^Y + X_{\text{zoo}}^Y \quad Y \in \{C, N, P\} \quad (1)$$

$$\frac{dY_{\text{phy}}}{dt} = V_{\text{phy}}^Y - I_{\text{phy}}^Y \cdot Q_{\text{phy}}^Y \quad Y \in \{C, N, P\} \quad (2)$$

$$\frac{d\text{Chl}}{dt} = \frac{dC_{\text{phy}}}{dt} \cdot \theta + \frac{d\theta}{dt} \cdot C_{\text{phy}} \quad (3)$$

$$\frac{dC_{\text{zoo}}}{dt} = V_{\text{zoo}}^C - I_{\text{zoo}}^C \quad (4)$$

where the superscripts denote the element (C, N, or P),  $V$  is assimilation into the state indicated by the subscript,  $I$  total ingestion by zooplankton of the compartment in the subscript,  $X$  is excretion,  $R$  respiration,  $Q$  the cell quota (N:C or P:C ratio,  $Q^C = 1$ ), and  $\theta$  the Chl:C<sub>phy</sub> ratio.

The individual fluxes in the right-hand sides of (1)–(4) 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, Dietze, and Oschlies, 2013; Pahlow and Prowe, 2010).

## 2 Chain-model for phytoplankton growth and diazotrophy

### 2.1 Trade-off between C and N assimilation

The trade-off between chlorophyll maintenance and nutrient acquisition introduced by Pahlow (2005) and Pahlow and Oschlies (2009) is replaced by a trade-off between chlorophyll maintenance and growth in Pahlow and Oschlies (2013) and Pahlow, Dietze, and Oschlies (2013). As did Wirtz and Pahlow (2010), the redesigned chain model makes use of allocation factors describing the fraction of cellular N allocated for specific tasks. The cost of chlorophyll maintenance ( $R^{\text{Chl}}$ ) is defined as

$$R^{\text{Chl}} = (L_d V_0^C S_I + R_M^{\text{Chl}}) \zeta^{\text{Chl}} \theta = f_C (L_d V_0^C S_I + R_M^{\text{Chl}}) \zeta^{\text{Chl}} \hat{\theta}, \quad f_C = \left(1 - \frac{Q_s^N}{Q^N} - f_V\right) \quad (2.1)$$

where  $f_V$  is the allocation factor for nutrient acquisition (uptake and assimilation),  $R_M^{\text{Chl}}$  the light-independent part of chlorophyll maintenance costs,  $Q_s^N$  the (non-allocatable) part of the N quota required for structural protein,  $\zeta^{\text{Chl}}$  the amount of fixed C respired per unit chlorophyll synthesised, and  $L_d$  day length as a fraction of 24 h. Nitrogen assimilation and temporally averaged net growth rate are

$$V^N = f_V \hat{V}^N \quad V_{\text{phy}}^N = C_{\text{phy}} \cdot V^N \quad (2.2)$$

$$\begin{aligned} \mu &= V^C - R, & V^C &= V_0^C f_C S_I, & R &= R^{\text{Chl}} + \zeta^N V_{\text{phy}}^N + R_M, \\ \Rightarrow \mu &= f_C \mathcal{A} - f_V \zeta^N \hat{V}^N - R_M, & V_{\text{phy}}^C &= C_{\text{phy}} \cdot \mu, & V_0^C &= \frac{V_0}{(0.5 + L_d)^{r_d}} \end{aligned} \quad (2.3)$$

where

$$S_I = 1 - \exp\left(-\frac{\alpha \hat{\theta} I}{V_0^C}\right), \quad \mathcal{A} = V_0^C S_I (1 - \zeta^{\text{Chl}} \hat{\theta}) - R_M^{\text{Chl}} \zeta^{\text{Chl}} \hat{\theta}, \quad \hat{\theta} = \frac{\theta}{f_C}, \quad (2.4)$$

and  $\theta$  is the Chl:C ratio. 24-h averages can be written as

$$\bar{\mu} = f_C \bar{\mathcal{A}} - f_V \zeta^N \hat{V}^N - R_M \quad \text{and} \quad \bar{\mathcal{A}} = L_d \cdot \mathcal{A} \quad (2.5)$$

Maximising  $\bar{\mu}$  with respect to  $\theta$  for balanced growth gives

$$\frac{d\bar{\mu}}{d\theta} \stackrel{!}{=} 0 \quad \Leftrightarrow \quad \frac{d\bar{\mathcal{A}}}{d\hat{\theta}} = L_d V_0^C \left[ \frac{\alpha I}{V_0^C} (1 - S_I) (1 - \zeta^{\text{Chl}} \hat{\theta}) - S_I \zeta^{\text{Chl}} \right] - R_M^{\text{Chl}} \zeta^{\text{Chl}} = 0 \quad (2.6)$$

$$\Leftrightarrow \quad 0 = L_d V_0^C \left\{ \frac{\alpha I}{V_0^C} \exp\left(-\frac{\alpha \hat{\theta} I}{V_0^C}\right) (1 - \zeta^{\text{Chl}} \hat{\theta}) - \left[1 - \exp\left(-\frac{\alpha \hat{\theta} I}{V_0^C}\right)\right] \zeta^{\text{Chl}} \right\} - R_M^{\text{Chl}} \zeta^{\text{Chl}} \quad (2.7)$$

$$\Leftrightarrow \quad \left( \frac{\alpha I}{V_0^C \zeta^{\text{Chl}}} - \frac{\alpha \hat{\theta} I}{V_0^C} + 1 \right) \exp\left(-\frac{\alpha \hat{\theta} I}{V_0^C}\right) - 1 = \frac{R_M^{\text{Chl}}}{L_d V_0^C} \quad (2.8)$$

$$\Leftrightarrow \quad \left( \frac{\alpha I}{V_0^C \zeta^{\text{Chl}}} - \frac{\alpha \hat{\theta} I}{V_0^C} + 1 \right) \exp\left(\frac{\alpha I}{V_0^C \zeta^{\text{Chl}}} + 1 - \frac{\alpha \hat{\theta} I}{V_0^C}\right) = \left(1 + \frac{R_M^{\text{Chl}}}{L_d V_0^C}\right) \exp\left(\frac{\alpha I}{V_0^C \zeta^{\text{Chl}}} + 1\right) \quad (2.9)$$

$$\Leftrightarrow \left( \frac{\alpha I}{V_0^C \zeta^{\text{Chl}}} - \frac{\alpha I \hat{\theta}}{V_0^C} + 1 \right) = W_0 \left[ \left( 1 + \frac{R_M^{\text{Chl}}}{L_d V_0^C} \right) \exp \left( 1 + \frac{\alpha I}{V_0^C \zeta^{\text{Chl}}} \right) \right] \quad (2.10)$$

$$\Leftrightarrow \hat{\theta} = \begin{cases} \frac{1}{\zeta^{\text{Chl}}} + \frac{V_0^C}{\alpha I} \left\{ 1 - W_0 \left[ \left( 1 + \frac{R_M^{\text{Chl}}}{L_d V_0^C} \right) \exp \left( 1 + \frac{\alpha I}{V_0^C \zeta^{\text{Chl}}} \right) \right] \right\} & \text{if } I > I_0 \\ 0 & \text{if } I \leq I_0 \end{cases} \quad (2.11)$$

where  $W_0$  is the 0-branch of the Lambert-W function, and the threshold irradiance  $I_0$  required to cover the light-independent cost of chlorophyll maintenance is given by

$$I_0 = \frac{\zeta^{\text{Chl}} R_M^{\text{Chl}}}{L_d \alpha}. \quad (2.12)$$

Chlorophyll dynamics drives the photo-acclimation process. Chlorophyll synthesis is assumed proportional to the current size of the chloroplast ( $f_C$ ) and must satisfy Eq. (2.11) at steady-state, which is accomplished by

$$\frac{\text{Chl}}{\text{Chl}} = \mu + \frac{\dot{\theta}}{\theta} = \mu + \frac{f_C}{\zeta^{\text{Chl}}} \frac{d\bar{\mu}}{d\theta} + f_C \cdot \frac{\tilde{Q}^N}{\theta} \frac{d\theta}{dQ^N} \quad (2.13a)$$

$$\frac{\text{Chl}}{\text{Chl}} = \mu + \frac{\dot{\theta}}{\theta} = \mu + \frac{f_C}{\zeta^{\text{Chl}}} \frac{d\bar{\mu}}{d\theta} \quad (2.13b)$$

where the dots indicate time derivatives and  $\mu$  is limited to positive values in the calculation of  $\tilde{Q}^N$  (Eq. 2.15) to prevent a positive feedback with Chl synthesis due to respiration caused by high  $\theta$ . Eq. (2.13b) represents slower Chl synthesis during periods of high rates of N acquisition. The photo-regulatory term,  $1/\zeta^{\text{Chl}} \cdot d\bar{\mu}/d\theta$ , is meant to represent adaptive dynamics and can be written as

$$\frac{1}{\zeta^{\text{Chl}}} \frac{d\bar{\mu}}{d\theta} = \frac{1}{\zeta^{\text{Chl}}} \frac{d\bar{\mu}}{d\hat{\theta}} \frac{d\hat{\theta}}{d\theta} = \frac{1}{\zeta^{\text{Chl}}} \frac{d\bar{\mathcal{A}}}{d\hat{\theta}} = L_d \left[ \alpha I (1 - S_I) \left( \frac{1}{\zeta^{\text{Chl}}} - \hat{\theta} \right) - S_I V_0^C \right] - R_M^{\text{Chl}} \quad (2.14)$$

and the relative change in  $\theta$  due to changing  $Q^N$  is

$$f_C \cdot \frac{\tilde{Q}^N}{\theta} \frac{d\theta}{dQ^N} = f_C \cdot \tilde{Q}^N \frac{\hat{\theta}}{\theta} \left( 2 \frac{Q_s^N}{Q^N} + \zeta^N \right) = \tilde{Q}^N \left( 2 \frac{Q_s^N}{Q^N} + \zeta^N \right), \quad \tilde{Q}^N = V_{\text{phy}}^N - \max(\mu, 0) \cdot Q \quad (2.15)$$

which accounts for the destruction and/or build-up of the chloroplast. Eq. (2.13a) is much faster than the Chl dynamics proposed in Pahlow (2005), which were developed to reproduce the rather long lag-phase reported for *Isochrysis galbana* by Flynn, Davidson, and Leftley (1994). However, recent simulations of mesocosm experiments have shown that a long lag-phase may not be typical for most plankton systems.

$Q^N$  can be eliminated from (2.3) with the help of the balanced-growth approximation:

$$Q^N = \frac{V_{\text{phy}}^N}{\bar{\mu} + R_M} = \frac{f_V \hat{V}^N}{\bar{\mathcal{A}} \left( 1 - \frac{Q_s^N}{Q^N} - f_V \right) - \zeta^N f_V \hat{V}^N} \quad (2.16)$$

$$\Leftrightarrow Q^N = \frac{\bar{\mathcal{A}} Q_s^N + f_V \hat{V}^N}{\bar{\mathcal{A}} (1 - f_V) - f_V \zeta^N \hat{V}^N} \quad (2.17)$$

$$\Leftrightarrow \bar{\mu} = \bar{\mathcal{A}} \left[ 1 - f_V - Q_s^N \frac{\bar{\mathcal{A}} (1 - f_V) - f_V \zeta^N \hat{V}^N}{\bar{\mathcal{A}} Q_s^N + f_V \hat{V}^N} \right] - f_V \zeta^N \hat{V}^N - R_M \quad (2.18)$$

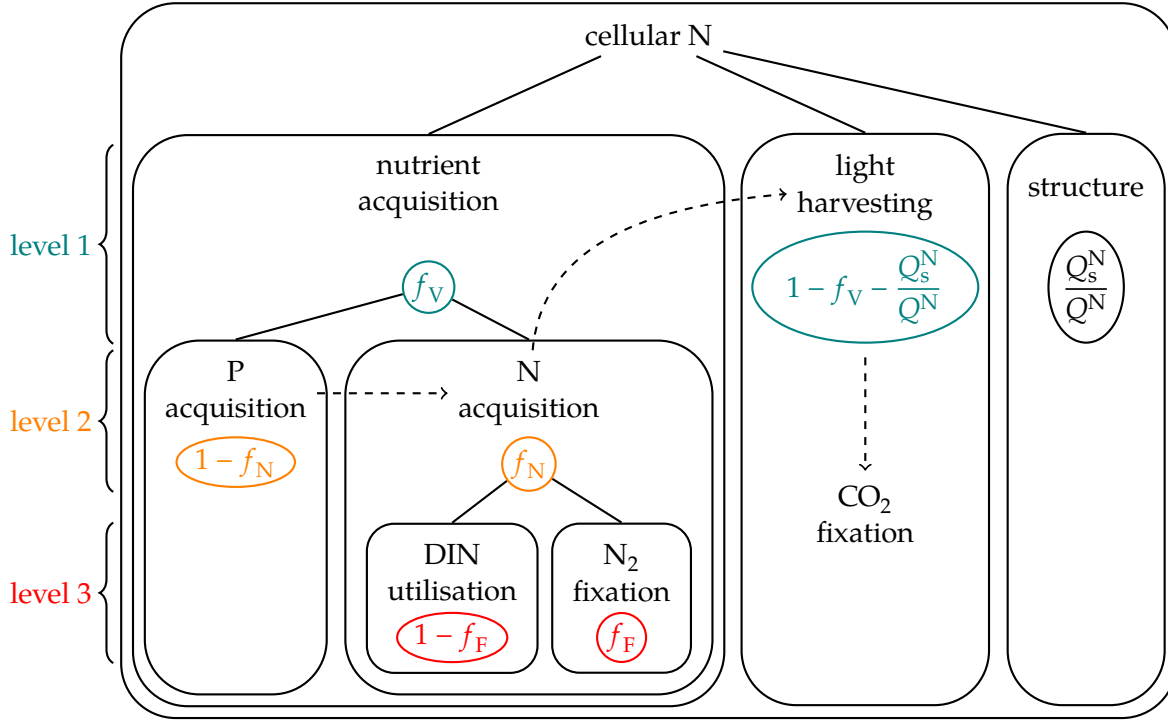


Figure 1: Orthogonal hierarchy of N allocation in the chain model.

$$= \left( \frac{\overline{\mathcal{A}}}{\overline{\mathcal{A}} + f_V \widehat{V}^N} \frac{1 - f_V + \zeta^N Q_s^N}{\overline{\mathcal{A}} + f_V \widehat{V}^N} - \zeta^N \right) f_V \widehat{V}^N - R_M \quad (2.19)$$

The optimal allocation of cellular N towards nutrient acquisition ( $f_V^0$ ) can be found by forming the derivative of  $\bar{\mu}$  with respect to  $f_V$  from (2.18):

$$\frac{d\bar{\mu}}{df_V} \stackrel{!}{=} 0 \quad \Leftrightarrow \quad f_V^{0^2} + 2f_V^0 \frac{\overline{\mathcal{A}} Q_s^N}{\widehat{V}^N} - \frac{\overline{\mathcal{A}}^2 Q_s^N}{\widehat{V}^N (\overline{\mathcal{A}} + \zeta^N \widehat{V}^N)} = 0 \quad (2.20)$$

$$\Leftrightarrow \quad f_V^0 = \frac{\overline{\mathcal{A}} Q_s^N}{\widehat{V}^N} \left[ -1 + \sqrt{1 + \frac{1}{Q_s^N \left( \frac{\overline{\mathcal{A}}}{\widehat{V}^N} + \zeta^N \right)}} \right] \quad (2.21)$$

## 2.2 Equivalence with Droop's cell-quota model

The problem with (2.21) is that it is an immediate function of current ambient light and nutrient availability, so that the regulation would likely end up trying to catch up with quickly-changing conditions. Given the balanced-growth assumption in the derivation of (2.21) this does not appear feasible. Thus, a regulation based solely on the internal physiological state defined by the composition of the cell is sought, implicitly responding to the average growth conditions during the last one or two generational cycles. In order to eliminate the nutrient- and light-dependent terms  $\widehat{V}^N$  and  $\overline{\mathcal{A}}$ , (2.17) is rearranged to find an expression for  $\overline{\mathcal{A}}/\widehat{V}^N$ , which is substituted in (2.20), whence (2.20) can be factorised as

$$\left[ f_V^0 - (1 + \zeta^N Q_s^N) \right] \left[ f_V^0 - \frac{Q_s^N}{Q^N} + \zeta^N (Q^N - 2Q_s^N) \right] = 0 \quad (2.22)$$

Table 1: Units and descriptions of symbols for phytoplankton

Symbol	Units	Description
$\alpha$	$\text{m}^2 \text{d E}^{-1} \text{molC gChl}^{-1}$	Chl-specific light absorption coefficient
$A_0$	$\text{m}^3 \text{molC}^{-1} \text{d}^{-1}$	potential nutrient affinity
$\zeta^{\text{Chl}}$	$\text{molC gChl}^{-1}$	cost of Chl synthesis
$\zeta^{\text{N}}$	$\text{molC molN}^{-1}$	cost of N assimilation
$F_0^{\text{N}}$	$\text{molC molC}^{-1} \text{d}^{-1}$	potential rate of $\text{N}_2$ fixation
$f_{\text{C}}$	—	N quota fraction allocated for $\text{CO}_2$ fixation
$f_{\text{F}}$	—	fraction of $f_{\text{N}} f_{\text{V}} Q^{\text{N}}$ allocated for $\text{N}_2$ fixation
$f_{\text{N}}$	—	fraction of $f_{\text{V}} Q^{\text{N}}$ allocated for N uptake
$f_{\text{V}}$	—	N quota fraction allocated for nutrient acquisition
$L_{\text{d}}$	—	day length as a fraction of 24 h
$\bar{\mu}$	$\text{d}^{-1}$	net growth rate averaged over 24 h
$N$	$\text{molN m}^{-3}$	DIN concentration
$P$	$\text{molN m}^{-3}$	DIP concentration
$Q^{\text{N}}$	$\text{molN molC}^{-1}$	N:C ratio (N quota)
$Q_{\text{s}}^{\text{N}}$	$\text{molN molC}^{-1}$	partial N quota associated with structural protein
$Q^{\text{P}}$	$\text{molP molC}^{-1}$	P:C ratio (P quota)
$Q_0^{\text{P}}$	$\text{molP molC}^{-1}$	subsistence P:C ratio (P quota)
$R$	$\text{d}^{-1}$	respiration
$R^{\text{Chl}}$	$\text{d}^{-1}$	respiration cost of Chl maintenance
$R_{\text{M}}$	$\text{d}^{-1}$	maintenance loss (same for C, N, P, Chl)
$R_{\text{M}}^{\text{Chl}}$	$\text{d}^{-1}$	Chl maintenance respiration
$r_{\text{DOC}}$	$\text{molC molC}^{-1} \text{d}^{-1}$	DOC release
$r_{\text{d}}$	—	daylength parameter
$S_{\text{I}}$	—	degree of light saturation
$\theta$	$\text{gChl molC}^{-1}$	Chl:C ratio
$\hat{\theta}$	$\text{gChl molC}^{-1}$	chloroplast Chl:C ratio
$V_0$	$\text{mol molC}^{-1} \text{d}^{-1}$	potential rate
$V^{\text{C}}$	$\text{molC molC}^{-1} \text{d}^{-1}$	gross C fixation rate
$V_0^{\text{C}}$	$\text{molC molC}^{-1} \text{d}^{-1}$	potential C fixation rate
$V_{\text{phy}}^{\text{N}}$	$\text{molN molC}^{-1} \text{d}^{-1}$	N uptake rate
$V_0^{\text{N}}$	$\text{molN molC}^{-1} \text{d}^{-1}$	potential N uptake rate
$V^{\text{P}}$	$\text{molP molC}^{-1} \text{d}^{-1}$	P uptake rate
$V_0^{\text{P}}$	$\text{molP molC}^{-1} \text{d}^{-1}$	potential P uptake rate

With the obvious condition  $0 < f_{\text{V}}^0 < 1$ , the second term has to be zero, i.e.,

$$f_{\text{V}}^0 = \frac{Q_{\text{s}}^{\text{N}}}{Q^{\text{N}}} - \zeta^{\text{N}}(Q^{\text{N}} - 2Q_{\text{s}}^{\text{N}}) \quad (2.23)$$

$\widehat{V}^N$  is eliminated from (2.3) with the help of

$$V_{\text{phy}}^N = f_V \widehat{V}^N = (\bar{\mu} + R_M) Q^N \quad (2.24)$$

and  $f_V^o$  from (2.23) is substituted for  $f_V$ , whereupon (2.3) becomes equivalent to Droop's (1974) cell-quota formula for balanced growth,

$$\bar{\mu} + R_M = \overline{\mathcal{A}} \left( 1 - 2 \frac{Q_s^N}{Q^N} \right). \quad (2.25)$$

where the subsistence quota is  $2Q_s^N$ .

Eq. (2.23) shows that the optimal balance between light harvesting and nutrient acquisition for balanced growth can be determined independently of external factors, i.e., nutrient concentrations and light intensity, which is not apparent in (2.21). The corollary is that an optimal regulation is possible which is robust to short-term variations in light and nutrient availability, since the nitrogen cell quota  $Q^N$  reflects a temporal average of growth conditions over a time scale of the order of one to several days. (2.23) is also very convenient for calculating the maximal  $Q^N$ , as defined by  $f_V^o = 0$ :

$$Q_{\text{max}}^N = \lim_{\widehat{V}^N \rightarrow \infty} Q^N = Q_0^N \left( 1 + \sqrt{1 + \frac{1}{\zeta^N Q_0^N}} \right), \quad (2.26)$$

which is identical to the expression found by Pahlow (2005).

The relationship between  $\bar{\mu}$  and  $f_V^o$  is found by solving (2.23) for  $Q^N$  and substituting in (2.25):

$$\bar{\mu} + R_M = \overline{\mathcal{A}} \left( 1 - \frac{2}{1 - \frac{f_V^o}{2\zeta^N Q_s^N} + \sqrt{\left( 1 - \frac{f_V^o}{2\zeta^N Q_s^N} \right)^2 + \frac{1}{\zeta^N Q_s^N}}} \right) \quad (2.27)$$

### 2.3 Nitrogen and phosphorus uptake

Both N and P uptake occur in the same compartment, which is allocated fraction  $f_V^o$  of available N resources. Resources are allocated between N and P uptake within the nutrient-assimilation compartment so that N assimilation is maximised. Since it follows from (2.25) that  $\bar{\mu}$  is uniquely related to  $Q^N$ , maximising  $\widehat{V}^N$  within the nutrient-assimilation compartment will maximise  $\bar{\mu}$  for the whole cell. N assimilation is determined by P availability in the cell:

$$V_{\text{phy}}^N = f_V^o \widehat{V}^N = f_V^o f_N \widehat{V}_*^N \quad V^P = f_V^o \widehat{V}^P = f_V^o (1 - f_N) \widehat{V}_*^P \quad (2.28)$$

$$\widehat{V}_*^N = \left( \sqrt{\frac{1}{V_{\text{max}}^N}} + \sqrt{\frac{1}{A_0 N}} \right)^{-2} \quad \widehat{V}_*^P = \left( \sqrt{\frac{1}{V_0^P}} + \sqrt{\frac{1}{A_0 P}} \right)^{-2} \quad (2.29)$$

$$V_{\text{max}}^N = V_0^N \left( 1 - \frac{Q_0^P}{Q^P} \right), \quad (2.30)$$

where  $N$  and  $P$  are DIN and DIP concentration and  $f_N$  is the allocation of resources for N uptake within the nutrient-assimilation compartment. In order to find the optimal allocation ( $f_N^o$ ),  $Q^P$  in (2.30) is replaced by the balanced-growth approximation

$$Q^P = Q^N \frac{V^P}{V_{\text{phy}}^N} = Q^N \left( \frac{1}{f_N} - 1 \right) \frac{\widehat{V}_*^P}{\widehat{V}_*^N}. \quad (2.31)$$

The system (2.28)–(2.31) can unfortunately not be transformed into an explicit steady-state equation for  $V_{\text{phy}}^N$ . Numerical solution of (2.29)–(2.31) given  $Q^N$  and  $f_N$  is straight forward, however, whence  $f_N^0$  is found numerically as well. A closed-form expression for  $f_N^0$  was obtained accidentally, starting with an attempt to find an approximation to  $f_N^0$  by solving

$$\frac{d\widehat{V}^N}{df_N} = \frac{\partial \widehat{V}^N}{\partial f_N} + \frac{\partial \widehat{V}^N}{\partial Q^P} \frac{dQ^P}{df_N} \stackrel{!}{=} 0, \quad (2.32)$$

$$\frac{dQ^P}{df_N} = \frac{\partial Q^P}{\partial f_N} + \frac{\partial Q^P}{\partial \widehat{V}_*^N} \frac{d\widehat{V}_*^N}{dQ^P} \frac{dQ^P}{df_N} \Leftrightarrow \frac{dQ^P}{df_N} = \frac{\frac{\partial Q^P}{\partial f_N}}{1 - \frac{\partial Q^P}{\partial \widehat{V}_*^N} \frac{d\widehat{V}_*^N}{dQ^P}}. \quad (2.33)$$

(2.33) is implicit because  $d\widehat{V}_*^N/dQ^P$  contains a circular dependence on  $dQ^P/df_N$ , but it proved fruitful to examine the approximation

$$\frac{dQ^P}{d\widehat{V}_*^N} \approx \frac{\partial Q^P}{\partial \widehat{V}_*^N}, \quad (2.34)$$

and making use of

$$\frac{\partial \widehat{V}^N}{\partial f_N} = \widehat{V}_*^N, \quad \frac{\partial \widehat{V}^N}{\partial Q^P} = \mathcal{B} f_N \frac{\widehat{V}_*^N}{Q^P}, \quad \frac{\partial Q^P}{\partial f_N} = -\frac{Q^N \widehat{V}_*^P}{f_N^2 \widehat{V}_*^N}, \quad (2.35)$$

where

$$\mathcal{B} = \frac{1}{\left(\frac{Q^P}{Q_0^P} - 1\right) \sqrt{\frac{V_0^N}{\widehat{V}_*^N} \left(1 - \frac{Q_0^P}{Q^P}\right)}} = \frac{1}{\left(\frac{Q^P}{Q_0^P} - 1\right) \sqrt{\frac{V_{\text{max}}^N}{\widehat{V}_*^N}}}. \quad (2.36)$$

Substituting (2.34)–(2.35) into (2.32) and solving for  $f_N$  does not yield an approximation to  $f_N^0$ , but, luckily, instead evaluates to a constant:

$$f_N = \frac{Q^N \widehat{V}_*^P}{Q^P \widehat{V}_*^N} \mathcal{B} \stackrel{!}{=} 1. \quad (2.37)$$

Thus, (2.37) can be solved for  $f_N^0$ , which indeed provides an exact solution of (2.32). (2.37) is multiplied with  $Q^P \widehat{V}_*^{N^2}$ , giving, with the help of (2.31),

$$\Leftrightarrow \mathcal{B} = \left(\frac{1}{f_N} - 1\right)^2 \frac{Q^N}{Q^P} \frac{\widehat{V}_*^P}{\widehat{V}_*^N} \quad (2.38)$$

$$\Leftrightarrow f_N^0 = \frac{1}{1 + \sqrt{\mathcal{B} \frac{\widehat{V}_*^N}{\widehat{V}_*^P} \frac{Q^P}{Q^N}}} = \frac{1}{1 + \sqrt{\frac{Q_0^P}{Q^N} \frac{V_0^N}{\widehat{V}_*^P} \left(\frac{\widehat{V}_*^N}{V_{\text{max}}^N}\right)^{1.5}}} = \frac{1 - \frac{Q_0^P}{Q^P}}{1 - \frac{Q_0^P}{Q^P} \left(1 - \sqrt{\frac{\widehat{V}_*^N}{V_{\text{max}}^N}}\right)}. \quad (2.39)$$

(2.39) is an implicit equation for balanced growth, since it involves  $Q^P$ , but can be applied directly in forward simulations, where  $Q^P$  is known. The last simplification is obtained by substituting  $Q^N$  from (2.37). If the system is not in steady state, (2.39) yields an approximation for  $f_N^0$  which converges towards the steady-state solution.

## 2.4 Transient down-regulation of C fixation

Because  $Q^P$  has no direct effect on  $\mu$ , the chain model faces the problem of outgrowing the P subsistence quota  $Q_0^P$  during intensifying P limitation ( $\dot{Q}^P < 0$ ). Hence, the down-regulation must respond specifically to declining  $Q^P$ . A relatively simple way to achieve the down-regulation is via the release of dissolved organic carbon (DOC) during the transition to P limitation. To this end,  $r_{\text{DOC}}$  is defined as a part of net C fixation being released as DOC:

$$\mu = V^C - R - r_{\text{DOC}}, \quad r_{\text{DOC}} = \max\left[\left(V^C - R\right)\frac{Q_0^P}{Q^P} - \frac{V^P}{Q_0^P}, 0\right] \cdot \max\left(2 - \frac{Q^P}{Q_0^P}, 0\right), \quad (2.40)$$

where  $\mu$  is instantaneous growth rate. Since  $V^C - R < V^P/Q_0^P$  for balanced growth, this should not affect the steady-state equations presented above. The factor  $Q_0^P/Q^P$  reduces DOC production. Other possibilities for the reduction term include  $\max(2 - Q^P/Q_0^P, 0)$ , restricting DOC release to  $Q_0^P \leq Q^P < 2Q_0^P$ , or  $\exp(1 - Q^P/Q_0^P)$ .

## 2.5 Calcification

Calcification is implemented as the product of a calcification factor ( $f_{\text{PIC}}$ ) and  $\text{CO}_2$  fixation:

$$V^{\text{PIC}} = f_{\text{PIC}} \cdot V^C \quad (2.41)$$

## 2.6 Nitrogen fixation

Nitrogen fixation is incorporated into the redesigned chain model as a new compartment dedicated to  $\text{N}_2$  fixation, which is separate from photosynthetic and nutrient uptake machineries. It is mathematically convenient to define the  $\text{N}_2$  fixation compartment as a fraction of the nitrogen assimilation machinery, i.e., a fraction of  $f_V \cdot f_N$ . Total nitrogen assimilation rate is then:

$$V_T^N = V_{\text{phy}}^N + F^N = f_V \widehat{V}_T^N = f_V f_N [(1 - f_F) \widehat{V}_*^N + f_F \widehat{F}_*^N], \quad (2.42)$$

where  $F^N$  and  $\widehat{F}_*^N$  are defined as  $\text{N}_2$  fixation relative to the whole cell and the  $\text{N}_2$  fixation compartment, respectively,

$$\widehat{F}_*^N = \left(1 - \frac{Q_0^P}{Q^P}\right) F_0^N, \quad (2.43)$$

and  $F_0^N$  is the potential  $\text{N}_2$  fixation rate of the  $\text{N}_2$  fixation apparatus. The energy requirement of  $\text{N}_2$  fixation incurs respiration costs  $\zeta^F F^N$ :

$$\bar{\mu} = \bar{\mathcal{A}} \left(1 - \frac{Q_s^N}{Q^N} - f_V\right) - f_V \bar{\zeta}^N \widehat{V}_T^N - R_M, \quad \bar{\zeta}^N = \frac{\zeta^N (1 - f_F) \widehat{V}_*^N + \zeta^F f_F \widehat{F}_*^N}{(1 - f_F) \widehat{V}_*^N + f_F \widehat{F}_*^N}, \quad (2.44)$$

where  $\zeta^F$  is the cost of  $\text{N}_2$  fixation and  $\bar{\zeta}^N$  the effective cost of N acquisition. Modifying Eqs. (2.17) and (2.21) to include  $\text{N}_2$  fixation gives

$$Q^N = \frac{\bar{\mathcal{A}} Q_s^N + f_V \widehat{V}_T^N}{\bar{\mathcal{A}} (1 - f_V) - f_V \bar{\zeta}^N \widehat{V}_T^N} = \frac{\bar{\mathcal{A}} Q_s^N + f_V \widehat{V}_T^N}{\bar{\mathcal{A}} - f_V (\bar{\mathcal{A}} + \bar{\zeta}^N \widehat{V}_T^N)} \quad (2.45)$$

$$f_V^o = \frac{\bar{\mathcal{A}} Q_s^N}{\widehat{V}_T^N} \left[ -1 + \sqrt{1 + \frac{1}{Q_s^N \left( \frac{\bar{\mathcal{A}}}{\widehat{V}_T^N} + \bar{\zeta}^N \right)}} \right]. \quad (2.46)$$



$\bar{\zeta}^N$  in (2.44) depends on  $f_N$  only through its effect on  $Q^P$ , which is ignored here for simplicity. The inaccuracy introduced thereby is of no consequence, as it will become clear below that (the exact form of) (2.54) is not needed. Thus,  $f_N^0$  is found by maximising  $\widehat{V}_T^N$  with respect to  $f_N$ , analogous to maximising  $\widehat{V}^N$  via (2.32)–(2.39):

$$\frac{d\widehat{V}_T^N}{df_N} = \frac{\partial\widehat{V}_T^N}{\partial f_N} + \left( \frac{\partial\widehat{V}_T^N}{\partial\widehat{V}_*^N} \frac{\partial\widehat{V}_*^N}{\partial Q^P} + \frac{\partial\widehat{V}_T^N}{\partial\widehat{F}_*^N} \frac{\partial\widehat{F}_*^N}{\partial Q^P} \right) \frac{dQ^P}{df_N} \stackrel{!}{=} 0, \quad (2.47)$$

$$\frac{dQ^P}{df_N} = \frac{\partial Q^P}{\partial f_N} + \frac{\partial Q^P}{\partial\widehat{V}_T^N} \frac{d\widehat{V}_T^N}{dQ^P} \frac{dQ^P}{df_N} \quad \Leftrightarrow \quad \frac{dQ^P}{df_N} = \frac{\frac{\partial Q^P}{\partial f_N}}{1 - \frac{\partial Q^P}{\partial\widehat{V}_T^N} \frac{d\widehat{V}_T^N}{dQ^P}}. \quad (2.48)$$

Now the same trick as above is applied to find an expression evaluating to one:

$$\frac{dQ^P}{df_N} \approx \frac{\partial Q^P}{\partial f_N} \quad (2.49)$$

$$\frac{\partial\widehat{V}_T^N}{\partial f_N} = \frac{\widehat{V}_T^N}{f_N}, \quad \frac{\partial\widehat{V}_T^N}{\partial\widehat{V}_*^N} = f_N(1 - f_F), \quad \frac{\partial\widehat{V}_T^N}{\partial\widehat{F}_*^N} = f_N f_F \quad (2.50)$$

$$\frac{\partial\widehat{F}_*^N}{\partial Q^P} = F_0^N \frac{Q_0^P}{Q^{P2}}, \quad \frac{\partial Q^P}{\partial f_N} = - \frac{Q^N \widehat{V}_*^P}{f_N^2 [(1 - f_F) \widehat{V}_*^N + f_F \widehat{F}_*^N]} \quad (2.51)$$

Solving (2.47) for  $f_N$  then yields, with  $\mathcal{B}$  as defined in (2.36),

$$f_N = \frac{Q^N}{Q^P} \widehat{V}_*^P \frac{(1 - f_F) \mathcal{B} + f_F F_0^N \frac{Q_0^P}{Q^P}}{[(1 - f_F) \widehat{V}_*^N + f_F \widehat{F}_*^N]^2} \stackrel{!}{=} 1 \quad (2.52)$$

which is expanded analogously to (2.37):

$$\Leftrightarrow \quad (1 - f_F) \mathcal{B} + f_F F_0^N \frac{Q_0^P}{Q^P} = \left( \frac{1}{f_N} - 1 \right)^2 \frac{Q^N}{Q^P} \widehat{V}_*^P, \quad (2.53)$$

$$\Leftrightarrow \quad f_N^0 = \frac{1}{1 + \sqrt{\frac{(1 - f_F) Q^P \mathcal{B} + f_F Q_0^P F_0^N}{Q^N \widehat{V}_*^P}}} = \frac{1}{1 + \sqrt{Q_0^P \frac{(1 - f_F) V_0^N (\widehat{V}_*^N / V_{\max}^N)^{1.5} + f_F F_0^N}{Q^N \widehat{V}_*^P}}}, \quad (2.54)$$

which is identical to (2.39) for  $f_F = 0$ .

## 2.7 Pure N<sub>2</sub> fixation

It follows immediately from (2.44) and (2.46) that for pure N<sub>2</sub> fixation, i.e.,  $N = 0$  or  $f_F = 1$ , the only further modification necessary is a reformulation of  $f_N^0$ :

$$Q^P = Q^N \frac{(1 - f_N) \widehat{V}_*^P}{\widehat{V}_T^N} = \frac{Q^N (1 - f_N) \widehat{V}_*^P}{f_N f_F \left( 1 - \frac{Q_0^P}{Q^P} \right) F_0^N} \quad \Leftrightarrow \quad Q^P = Q_0^P + Q^N \left( \frac{1}{f_N} - 1 \right) \frac{\widehat{V}_*^P}{f_F F_0^N} \quad (2.55)$$

$$\widehat{V}_T^N = f_N f_F \left[ 1 - \frac{Q_0^P}{Q_0^P + \frac{Q^N (1 - f_N) \widehat{V}_*^P}{f_N f_F F_0^N}} \right] F_0^N = \frac{1}{\frac{Q_0^P}{(1 - f_N) Q^N \widehat{V}_*^P} + \frac{1}{f_N f_F F_0^N}} \quad (2.56)$$

$$\frac{d\widehat{V}_T^N}{df_N} \stackrel{!}{=} 0 \quad \Leftrightarrow \quad f_N^o = \frac{1}{1 + \sqrt{f_F \frac{Q_0^P F_0^N}{Q^N \widehat{V}_*^P}}} = 1 - \frac{Q_0^P}{Q^P}, \quad (2.57)$$

where the last simplification was achieved by substituting  $Q^N$  from (2.52). The shape of (2.57) is the same as that of (2.54) for  $N = 0$ . Substituting (2.57) back into (2.56) allows solving (2.55)–(2.57) directly for  $P$  limited continuous cultures:

$$\widehat{V}_T^N = \left( \sqrt{\frac{Q_0^P}{Q^N \widehat{V}_*^P}} + \sqrt{\frac{1}{f_F F_0^N}} \right)^{-2} \quad (2.58)$$

$$\Leftrightarrow \quad \widehat{V}_*^P = \frac{Q_0^P}{Q^N} \left( \sqrt{\frac{1}{\widehat{V}_T^N}} - \sqrt{\frac{1}{f_F F_0^N}} \right)^{-2}, \quad Q^N = \frac{2Q_s^N}{1 - \frac{\bar{\mu} + R_M}{\mathcal{A}}} \quad (2.59)$$

$$\Leftrightarrow \quad P = \frac{1}{A_0} \left[ \sqrt{\frac{Q^N}{Q_0^P}} \left( \sqrt{\frac{1}{\widehat{V}_T^N}} - \sqrt{\frac{1}{f_F F_0^N}} \right) - \sqrt{\frac{1}{V_0^P}} \right]^{-2}, \quad \widehat{V}_T^N = \frac{(\bar{\mu} + R_M) Q^N}{f_V^o}. \quad (2.60)$$

Substituting (2.57) into (2.55) yields a relatively simple expression for  $Q^P$ :

$$Q^P = Q_0^P + \sqrt{Q^N Q_0^P \frac{\widehat{V}_*^P}{f_F F_0^N}} \quad (2.61)$$

Fig. 2 compares model predictions with observations for pure  $N_2$  fixation, i.e., without DIN in the supply, for *Trichodesmium erythraeum*. Since both datasets shown in Fig. 2 were obtained with the same species, only a single parameter set was used (Table 2). Interestingly, parameter estimates suggest that all three of  $V_0^N$ ,  $V_0^P$  and  $V_0^C$  can be replaced by a single potential-rate parameter,  $V_0$ , except the temperature dependence,  $f(T)$ , and that  $V_0^C$  varies as a function of daylength in (2.3):

$$V_0^C = f(T) \cdot \frac{V_0}{(0.5 + L_d)^{r_d}}, \quad V_0^N = f(T) \cdot V_0, \quad V_0^P = f(T) \cdot V_0 \quad (2.62)$$

where  $r_d$  is the daylength parameter, which can vary between 0 and 1. For  $r_d = 0$ ,  $V_0^C$  is independent of daylength. The model simulations for the two experiments only differ in DIP concentration in the supply and light intensity. Obviously the model cannot reproduce POP concentrations greater than the DIP concentration in the supply (Fig. 2B), which could point to measurement problems or indicate that a true steady state was not achieved in the chemostat.

## 2.8 Time and depth averages of $S_I$

In order to account for the decline in light intensity with depth  $d$ , the depth-average of  $S_I$  can be obtained from its depth-integral with the help of the exponential-integral function (Ei):

$$I(d) = I_0 e^{-\varepsilon(\text{Chl}) \cdot d} \quad \Rightarrow \quad S_I(d) = 1 - e^{-\hat{\alpha} I_0 e^{-\varepsilon(\text{Chl}) \cdot d}}, \quad \hat{\alpha} = \frac{\alpha \hat{\theta}}{V_0^C} \quad (2.63)$$

$$\overline{S_I}^d = \frac{1}{d_1 - d_0} \int_{d_0}^{d_1} S_I(d) dd = 1 - \frac{\text{Ei}[-\hat{\alpha} I(d_0)] - \text{Ei}[-\hat{\alpha} I(d_1)]}{\varepsilon(\text{Chl}) \cdot (d_1 - d_0)} \quad (2.64)$$

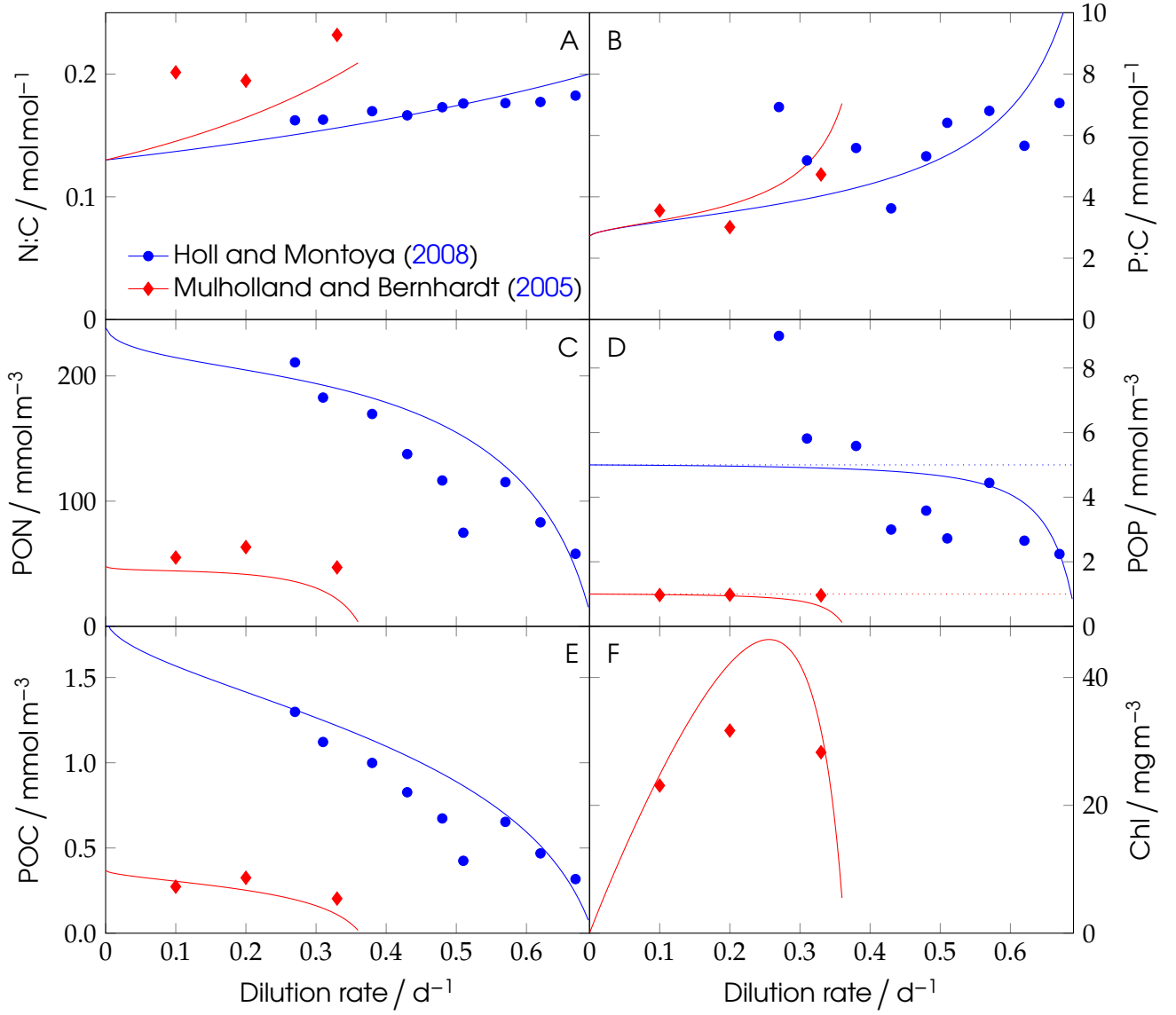


Figure 2: Fit of optimal N<sub>2</sub> fixation to observations from Mulholland and Bernhardt (2005) and Holl and Montoya (2008). The thin dotted lines in panel D indicate P concentrations in the supply. Parameter settings for *Trichodesmium* sp. from Table 2.

where  $\overline{S}_1^d$  is the depth-average of  $S_1$  in a layer ranging in depth from  $d_0$  to  $d_1$ , and  $\varepsilon(\text{Chl})$  is the Chl-dependent light-attenuation coefficient. When the diurnal light cycle is not resolved, it is most convenient to use the steady-state solution for  $\hat{\theta}$  and approximate the diurnal light cycle with a triangular light function. With  $\overline{I}_0$  and  $\overline{I}_1$  defined as the mean daytime irradiances at depths  $d_0$  and  $d_1$ ,

$$\overline{I}_1 = \overline{I}_0 e^{-\varepsilon(\text{Chl}) \cdot (d_1 - d_0)} \quad (2.65)$$

Table 2: Parameter estimates for *Trichodesmium* (Figs. 2), the non-diazotrophic cyanobacterium *Synechococcus linearis*, and the diatom *Thalassiosira fluviatilis*.

Parameter	<i>Trichodesmium</i> sp.	<i>S. linearis</i>	<i>T. fluviatilis</i>	Units
$A_0$	60	90	70	$\text{m}^3 \text{molC}^{-1} \text{d}^{-1}$
$\alpha$	3.7	1.4	1.6	$\text{m}^2 \text{d E}^{-1} \text{molC gChl}^{-1}$
$Q_s^N$	0.065	0.043	0.023	$\text{molN molC}^{-1}$
$Q_0^P$	0.0027	0.0012	0.0008	$\text{molP molC}^{-1}$
$V_0$	5	5	5	$\text{mol molC}^{-1} \text{d}^{-1}$
$R_M$	0	0	0	$\text{d}^{-1}$
$R_M^{\text{Chl}}$	0.1	0.1	0.1	$\text{d}^{-1}$
$\zeta^{\text{Chl}}$	0.6	0.4	0.55	$\text{molC gChl}^{-1}$
$\zeta^N$	0.7	0.6	0.75	$\text{molC molN}^{-1}$
$F_0^N$	1.3	—	—	$\text{molN molC}^{-1} \text{d}^{-1}$
$\zeta^F$	2	—	—	$\text{molC molN}^{-1}$

the depth- and time-averaged light saturation is (stem functions in (2.64) and (2.66) from <http://integrals.wolfram.com>):

$$\begin{aligned}
 \bar{S}_I &= \int_0^1 1 - \frac{\text{Ei}(-2\hat{\alpha}\bar{I}_0x) - \text{Ei}(-2\hat{\alpha}\bar{I}_1x)}{\varepsilon(\text{Chl}) \cdot (d_1 - d_0)} dx \\
 &= \left[ x \left( 1 - \frac{\text{Ei}(-2\hat{\alpha}\bar{I}_0) - \text{Ei}(-2\hat{\alpha}\bar{I}_1)}{\varepsilon(\text{Chl}) \cdot (d_1 - d_0)} \right) - \frac{e^{-2\hat{\alpha}\bar{I}_0x}/\bar{I}_0 - e^{-2\hat{\alpha}\bar{I}_1x}/\bar{I}_1}{2\hat{\alpha} \cdot \varepsilon(\text{Chl}) \cdot (d_1 - d_0)} \right]_0^1 \\
 &= 1 - \frac{\text{Ei}(-2\hat{\alpha}\bar{I}_0) - \text{Ei}(-2\hat{\alpha}\bar{I}_1)}{\varepsilon(\text{Chl}) \cdot (d_1 - d_0)} - \frac{(1 - e^{-2\hat{\alpha}\bar{I}_1})/\bar{I}_1 - (1 - e^{-2\hat{\alpha}\bar{I}_0})/\bar{I}_0}{2\hat{\alpha} \cdot \varepsilon(\text{Chl}) \cdot (d_1 - d_0)}
 \end{aligned} \tag{2.66}$$

where the factor 2 converts the mean to the maximum in the triangular light cycle. The mean daytime irradiance is the ratio of the mean daily (24 h) irradiance and daylength fraction  $L_d$ .

### 3 Zooplankton

The C:N:P stoichiometry of the phytoplankton compartment varies and is generally different from the (constant) composition of the zooplankton. 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

$$f_Q = \min \left( \frac{\Pi^N}{\Pi^C Q_{\text{zoo}}^N}, \frac{\Pi^P}{\Pi^C Q_{\text{zoo}}^P}, 1 \right), \quad \Pi^n = \phi_0 \cdot \sum_{i \in \{\text{bac}, \text{phy}, \text{det}, \text{zoo}\}} \phi_i n_i, \quad n \in \{\text{C}, \text{N}, \text{P}\} \tag{3.1}$$

Zooplankton net growth ( $V_{\text{zoo}}^C$ ) is the difference between assimilation and respiration costs of foraging, assimilation, and maintenance, corrected for the stoichiometric imbalance and fish mortality in the surface layer,

$$V_{\text{zoo}}^C = [EI^C(1 - c_a) - C_{\text{zoo}}(c_f A_F + f_{\text{zoo}}^T R_M)] f_Q - M_{\text{fish}} \cdot C_{\text{zoo}}, \quad E = E_{\text{max}} \left[ 1 - e^{-\beta \left( \frac{A_T}{A_F} - 1 \right)} \right] \tag{3.2}$$

where  $E$  is assimilation efficiency,  $c_a$  and  $c_f$  are the cost of assimilation and foraging coefficients,  $I^C$  total C ingestion,  $R_M$  maintenance respiration,  $E_{\max} = 1$  maximum assimilation efficiency,  $\beta = 0.2$  the digestion coefficient, and  $A_T$  and  $A_F$  total and foraging activity, respectively. Foraging activity and effective prey concentration,  $\Pi^C$ , determine  $I^C$ :

$$I^C = C_{\text{zoo}} A_F \hat{I}, \quad \hat{I} = 1 - e^{-\Pi^C} \quad (3.3)$$

where  $\hat{I}$  is ingestion saturation,  $\phi_0$  the potential prey capture coefficient, and  $\phi_i$  and  $C_i$  are the food preference for and biomass concentration of prey type  $i$  (phytoplankton, zooplankton). Ingestion of individual prey types is then

$$I_i^C = \frac{\phi_i C_i}{\Pi^C} I^C, \quad i \in \{\text{bac, phy, det, zoo}\} \quad (3.4)$$

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

$$A_F = \begin{cases} \frac{\beta A_T}{-1 - W_{-1} \left\{ - \left[ 1 - \frac{c_f}{E_{\max} \hat{I} (1 - c_a)} \right] e^{-(1+\beta)} \right\}} & \text{if } \Pi^C > \Pi_{\text{th}} \\ 0 & \text{if } \Pi \leq \Pi_{\text{th}} \end{cases} \quad (3.5)$$

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

$$\Pi_{\text{th}} = \ln \frac{1}{1 - \frac{c_f}{E_{\max}(1 - c_a)}} \quad (3.6)$$

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

$$A_T = f_{\text{zoo}}^T \frac{I_{\max}}{\beta} \left\{ -1 - W_{-1} \left[ - \left( 1 - \frac{c_f}{E_{\max} (1 - c_a)} \right) e^{-(1+\beta)} \right] \right\} \quad (3.7)$$

See Pahlow and Prowe (2010) for the derivation of (3.2)–(3.7) and more details. The release of C, N, and P comprises (dissolved inorganic) excretion ( $R$ ) and (particulate or dissolved organic) egestion ( $X$ ):

$$R_{\text{zoo}}^C = E I^C - V_{\text{zoo}}^C - M_{\text{fish}} \cdot C_{\text{zoo}} \quad X_{\text{zoo}}^C = I^C (1 - E) + M_{\text{fish}} \cdot C_{\text{zoo}} \quad (3.8)$$

$$R_{\text{zoo}}^n = \frac{I^C \frac{\Pi^n}{\Pi^C} - V_{\text{zoo}}^n Q_{\text{zoo}}^n}{1 + \frac{X_{\text{zoo}}^C}{R_{\text{zoo}}^C}} \quad X_{\text{zoo}}^n = R_{\text{zoo}}^n \frac{X_{\text{zoo}}^C}{R_{\text{zoo}}^C}, \quad n \in \{N, P\} \quad (3.9)$$

Fraction  $f_{\text{diss}}^X$  of the egestion ( $X$ ) ends up in the DOM and  $1 - f_{\text{diss}}^X$  enters the detritus compartment.

### 3.1 Zooplankton diel vertical migration

Diel vertical migration (dvm) moves zooplankton down around sunrise and back to the surface around sunset. Dvm is implemented by calculating vertical velocities ( $v_{\text{zoo}}$ ) in levels above the day-time depth ( $d_{\text{day}}$ ):

$$x_{\text{down}} = \max(\Delta t_{\text{dvm}} - |t - t_{\text{sunrise}}|, 0)^8 \quad (3.10)$$

$$x_{\text{up}} = \max(\Delta t_{\text{dvm}} - |t - t_{\text{sunset}}|, 0)^8 \quad (3.11)$$

$$v_{\text{zoo}} = v_{\text{dvm}} \cdot \left\{ \frac{x_{\text{down}}}{x_{\text{down}} + 1 \text{ day}} - \frac{x_{\text{up}}}{x_{\text{up}} + 1 \text{ day}} \cdot \min \left[ 2 \cdot \max \left( 1 - \frac{d_{\text{night}}}{d}, 0 \right), 1 \right] \right\} \quad (3.12)$$

where  $d_{\text{night}}$  is the night-time target depth and  $v_{\text{dvm}}$  the maximal migration velocity for dvm. This seems to work well only with the upwind advection scheme.

Table 3: Units and definitions of symbols for zooplankton

Symbol	Units	Definition
$A_f$	$d^{-1}$	foraging activity
$A_T$	$d^{-1}$	potential total activity
$\beta$		digestion coefficient
$c_a$		cost of assimilation
$c_f$		cost of foraging
$d_{\text{summer}}, d_{\text{winter}}$	m	summer, winter depth of svm
$\text{doy}_{\text{asc}}, \text{doy}_{\text{des}}$	doy	day of year of ascent, descent
$\mathcal{D}_{\text{asc}}, \mathcal{D}_{\text{des}}$	$\text{molC doy m}^{-3}$	$C_{\text{zoo}} \cdot \text{doy}_{\text{asc}}, C_{\text{zoo}} \cdot \text{doy}_{\text{des}}$
$\Delta t_{\text{svm}}$	d	width of time window for svm
$E_{\text{max}}, E$		maximum, actual assimilation efficiency
$f_Q$		cell-quota factor
$f_{\text{zoo}}^T$		zooplankton temperature dependence
$f_{\text{diss}}^X$		fraction of dissolved egestion
$h$	m	height of current layer
$I^C$	$\text{molC m}^{-3} d^{-1}$	rate of ingestion
$\hat{I}$		ingestion saturation
$M_{\text{fish}}$	$d^{-1}$	mortality in the surface layer due to fish
$\phi_0$	$\text{m}^3 \text{molC}^{-1}$	potential prey-capture coefficient
$\phi_i$		food preferences, $i \in \{\text{bac}, \text{phy}, \text{det}, \text{zoo}\}$
$\Pi^n$		effective prey concentration, $n \in \{C, N, P\}$
$\Pi_{\text{th}}$		effective feeding threshold
$Q_x^N, Q_x^P$	$\text{mol molC}^{-1}$	N:C, P:C ratio of $x$ , $x \in \{\text{bac}, \text{phy}, \text{det}, \text{zoo}\}$
$R_M$	$d^{-1}$	maintenance respiration
$R_{\text{zoo}}^n$	$\text{mol m}^{-3} d^{-1}$	zooplankton excretion, $n \in \{C, N, P\}$
$t_y$	doy	current time of the year
$V_{\text{zoo}}^C$	$d^{-1}$	zooplankton net growth rate
$v_{\text{svm}}$	$\text{m d}^{-1}$	potential zooplankton vertical velocity during svm
$v_{\text{zoo}}$	$\text{m d}^{-1}$	zooplankton vertical velocity
$\mathcal{V}_{\text{zoo}}$	$\text{m d}^{-1}$	apparent vertical velocity of $\mathcal{D}_{\text{asc}}$ or $\mathcal{D}_{\text{des}}$
$X_{\text{zoo}}^n$	$\text{mol m}^{-3} d^{-1}$	zooplankton egestion, $n \in \{C, N, P\}$

### 3.2 Zooplankton seasonal vertical migration

Seasonal vertical migration (svm) is implemented via four traits, the days of the year (doy) of ascent and descent ( $\text{doy}_{\text{asc}}$  and  $\text{doy}_{\text{des}}$ ), and the summer and winter depths ( $d_{\text{summer}}$  and  $d_{\text{winter}}$ ). The maximum vertical velocity of the migration ( $v_{\text{svm}}$ ) is assumed constant, but the motions ramp up smoothly a few days before and fade out a few days after the actual days of the svm. This is achieved by calculating the

vertical velocity of the zooplankton ( $v_{\text{zoo}}$ ) as

$$v_{\text{zoo}} = v_{\text{svm}} \cdot \left[ \exp \left( - \left| \frac{t_y - \text{doy}_{\text{des}}}{\Delta t_{\text{svm}}} \right|^8 - \left| \frac{d}{d_{\text{winter}}} \right|^{16} \right) \cdot \min \left( \frac{{}^{(-1)}C_{\text{zoo}}}{C_{\text{th}}}, 1 \right) - \exp \left( - \left| \frac{t_y - \text{doy}_{\text{asc}}}{\Delta t_{\text{svm}}} \right|^8 - \left| \frac{d - d_{\text{winter}} - d_{\text{summer}}}{d_{\text{winter}} - 0.5 d_{\text{summer}}} \right|^{16} \right) \cdot \min \left( \frac{{}^{(+1)}C_{\text{zoo}}}{C_{\text{th}}}, 1 \right) \right] \quad (3.13)$$

where the first term describes the descent in autumn ( $v_{\text{svm}} > 0$ ) and the second the ascent in spring ( $v_{\text{svm}} < 0$ ).  $\Delta t_{\text{svm}}$  defines the width of the time-window for the svm,  $t_y$  is the current time of the year in units of days,  $C_{\text{th}}$  is a threshold concentration, and  ${}^{(-1)}C_{\text{zoo}}$  and  ${}^{(+1)}C_{\text{zoo}}$  are the zooplankton concentrations above and below the current layer boundary. The reduction of the vertical velocity below the threshold concentration is necessary for numerical stability.

### 3.2.1 Hibernation

During hibernation, maintenance costs may be reduced by stopping all foraging activity. This is implemented by applying hibernation factors ( $f_{\text{hib}}$ ) at the hibernation depth ( $z_{\text{hib}}$ ) of the seasonal migrators.

$$R_{\text{M}} = \begin{cases} f_{\text{hib}}^{\text{R}} \cdot R_{\text{M}}^0 & \text{if } z = z_{\text{hib}} \\ R_{\text{M}}^0 & \text{otherwise} \end{cases} \quad (3.14)$$

$$\phi = \begin{cases} 0 & \text{if } f_{\text{hib}}^{\text{R}} < 1 \text{ and } z = z_{\text{hib}} \\ \phi^0 & \text{otherwise} \end{cases} \quad (3.15)$$

where  $\phi^0$  and  $R_{\text{M}}^0$  are the default values of  $\phi$  and  $R_{\text{M}}$ , respectively.

### 3.2.2 Days of ascent and descent as dynamic traits

Traits are stored in OPPLA as tracer-trait products, which can be treated mostly as regular (material) tracers in terms of advection and diffusion (mixing). The svm traits are defined as

$$\mathcal{D}_{\text{asc}} = C_{\text{zoo}} \cdot \text{doy}_{\text{asc}} \quad (3.16)$$

$$\mathcal{D}_{\text{des}} = C_{\text{zoo}} \cdot \text{doy}_{\text{des}} \quad (3.17)$$

It was impossible to obtain stable simulations with the modified central differencing scheme for vertical motions apparently as a consequence of the tight feed-back between changes in  $\text{doy}_{\text{asc}}$ ,  $\text{doy}_{\text{des}}$  and the vertical velocity. Thus, the boundary concentrations of  $\mathcal{D}_{\text{asc}}$  and  $\mathcal{D}_{\text{des}}$  are obtained as the products of the corresponding upwind doy and central  $C_{\text{zoo}}$ :

$${}^{(0)}\mathcal{D}_x = \begin{cases} {}^{(0)}C_{\text{zoo}} \cdot {}^{(-1)}\text{doy}_x & \text{for } v_{\text{zoo}} > 0 \\ {}^{(0)}C_{\text{zoo}} \cdot {}^{(+1)}\text{doy}_x & \text{for } v_{\text{zoo}} < 0 \end{cases}, \quad x \in \{\text{asc}, \text{des}\} \quad (3.18)$$

where the left superscripts indicate quantities at the boundary (0) and in the adjacent upper (−1) and lower (+1) layers.

Zooplankton net growth introduces changes in  $\mathcal{D}_{\text{asc}}$  and  $\mathcal{D}_{\text{des}}$ ,

$$\dot{\mathcal{D}}_x = V_{\text{zoo}}^{\text{C}} \cdot \text{doy}_x, \quad x \in \{\text{asc}, \text{des}\} \quad (3.19)$$

which keep  $\text{doy}_{\text{asc}}$  and  $\text{doy}_{\text{des}}$  steady. Trait variations (in  $\text{doy}_{\text{asc}}$  and  $\text{doy}_{\text{des}}$ ) result from the assumption that the animals take the current time of the year ( $t_y$ ) with them as their day of ascent or descent when

leaving their winter or summer depth, respectively. It is further assumed here that the trait distribution of the remaining population is unaffected by this process. This (passive) change of the traits is implemented by modifying  $\dot{\mathcal{D}}_{\text{asc}}$  and  $\dot{\mathcal{D}}_{\text{des}}$  adjacent to the summer or winter layers in the direction of migration:

$${}^{(-1)}\dot{\mathcal{D}}_{\text{asc}} = {}^{(-1)}\dot{\mathcal{D}}_{\text{asc}} - \begin{cases} ({}^{(0)}C_{\text{zoo}} \cdot t_y - {}^{(0)}\mathcal{D}_{\text{asc}}) \cdot \frac{v_{\text{zoo}}}{({}^{(-1)}h)} & \text{for } v_{\text{zoo}} < 0 \quad \wedge \quad d \approx d_{\text{winter}} \\ 0 & \text{otherwise} \end{cases} \quad (3.20)$$

$${}^{(+1)}\dot{\mathcal{D}}_{\text{des}} = {}^{(+1)}\dot{\mathcal{D}}_{\text{des}} + \begin{cases} ({}^{(0)}C_{\text{zoo}} \cdot t_y - {}^{(0)}\mathcal{D}_{\text{asc}}) \cdot \frac{v_{\text{zoo}}}{({}^{(+1)}h)} & \text{for } v_{\text{zoo}} > 0 \quad \wedge \quad d \approx d_{\text{summer}} \\ 0 & \text{otherwise} \end{cases} \quad (3.21)$$

where  ${}^{(-1)}h$  and  ${}^{(+1)}h$  are the heights of the adjacent layers and the  $\approx$  symbol indicates that the calculation is applied only for the layer encompassing  $d_{\text{summer}}$  or  $d_{\text{winter}}$ .

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