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# A Process Model: Supplementary Material

## A.1 A simple adaptive model of phytoplankton growth and composition in response to light, nutrient, and temperature.

The phytoplankton growth model used in this paper predicts changes in phytoplankton specific growth rate  $g$  and composition (nitrogen:carbon chlorophyll-a:carbon ratios) in response to changes in incident irradiance  $E$ , temperature  $T$ , and dissolved inorganic nitrogen  $N$ . The formulation represents a compromise between realism and complexity. Consistent with the BHM framework, we have sought a formulation that explicitly connects the key observed quantity chlorophyll-a ( $Chla$ ) to the state variable of phytoplankton biomass ( $P$ ) using the common currency of nitrogen. By explicitly treating changes in nitrogen:carbon ratios as well, the formulation would also support observations of dissolved oxygen or dissolved inorganic carbon, although we do not treat those in this paper. At the same time, we have avoided introducing additional hidden state variables, and we have sought to minimize the number of new parameters. This formulation draws on the adaptive phytoplankton growth model of Geider et al. (1998), who specified the carbon-specific phytoplankton growth rate,  $g_C$ , and the nitrogen-specific phytoplankton growth rate,  $g_N$ , as follows:

$$g_C = g_C^m \cdot (1 - \exp(-\alpha \cdot \lambda \cdot E / g_C^m)), \quad (\text{A.1})$$

$$g_C^m = g^{max} \cdot Tc \cdot (\chi - \chi^{min}) / (\chi^{max} - \chi^{min}), \quad (\text{A.2})$$

$$g_N = V^m \cdot N / (K + N), \quad (\text{A.3})$$

$$V^m = V^{max} \cdot Tc \cdot (\chi^{max} - \chi) / (\chi^{max} - \chi^{min}). \quad (\text{A.4})$$

Here, the temperature correction factor  $Tc$  is based on a “ $Q_{10}$  factor” (see Eq. (10) in the main text),  $\lambda$  is the chlorophyll-a:carbon ratio,  $K$  is the half-saturation constant for phytoplankton growth on  $N$ , and  $\alpha$  is the initial slope of the photosynthesis versus irradiance curve. In Geider et al. (1998)’s model, the light-saturated  $C$ -specific phytoplankton growth rate,  $g_C^m$ , and the nutrient-saturated phytoplankton nitrogen-specific growth rate,  $V^m$ , depend on the nitrogen:carbon ratio,  $\chi$ , in a way that ensures that the ratio lies between  $\chi^{min}$  and  $\chi^{max}$ . We may think of this formulation as an extensive version of a cell quota model.

Geider et al. (1998) introduced a third expression for the phytoplankton *Chla*-specific growth rate,  $g_{Chl}$ , as a function of  $g_C$ ,  $g_N$ ,  $\lambda$ ,  $E$ , and  $\chi$ . Here, we have avoided introducing new dynamic state variables for phytoplankton carbon and phytoplankton chlorophyll-a. Instead, we have sought a solution for  $g_N$ ,  $\lambda$  and  $\chi$ , as functions of  $T$ ,  $N$  and  $E$ , under conditions of balanced growth when  $g_C = g_N = g_{Chla}$ . It is not possible to derive an explicit expression for these solutions in the original model. However, it is possible to do so with the following key simplification.

Behrenfeld et al. (2005) argue that phytoplankton adjust their chlorophyll-a:carbon ratio,  $\lambda$ , so that it is proportional to  $g_C^m$  under balanced growth. We assume that, at steady-state,

$$\lambda = \lambda^{max} \cdot g_C^m / g^{max}, \quad (\text{A.5})$$

35 and substituting (A.5) into (A.1) gives

$$g_C = g_C^m \cdot (1 - \exp(-\alpha \cdot \lambda^{max} \cdot E / g^{max})). \quad (\text{A.6})$$

36 We define  $g_E^*$  as the maximum  $C$ -specific phytoplankton growth rate for given irradiance  $E$   
 37 and temperature  $T$ . This is achieved at  $\chi = \chi^{max}$  and is given by:

$$g_E^* = g^{max} \cdot Tc \cdot (1 - \exp(-\alpha \cdot \lambda^{max} \cdot E / g^{max})). \quad (\text{A.7})$$

38 We define  $g_N^*$  as the maximum  $N$ -specific phytoplankton growth rate for given nutrient  
 39 concentration  $N$  and temperature  $T$ . This is achieved at  $\chi = \chi^{min}$  and is given by:

$$g_N^* = V^{max} \cdot Tc \cdot N / (K + N). \quad (\text{A.8})$$

40 Now,  $g_C = g_E^* \cdot (\chi - \chi^{min}) / (\chi^{max} - \chi^{min})$ , and  $g_N = g_N^* \cdot (\chi^{max} - \chi) / (\chi^{max} - \chi^{min})$ .

41 Under balanced growth, the specific growth rate  $g = g_C = g_N$ , and solving for  $\chi$  gives:

$$\chi = (g_E^* \cdot \chi^{min} + g_N^* \cdot \chi^{max}) / (g_E^* + g_N^*). \quad (\text{A.9})$$

42 Substituting (A.9) into  $g_C = g_E^* \cdot (\chi - \chi^{min}) / (\chi^{max} - \chi^{min})$ , and appealing to the equality

43  $g = g_C = g_N$ , yields:

$$g = g_E^* \cdot g_N^* / (g_E^* + g_N^*) \quad (\text{A.10})$$

44 and, from, (A.5)

$$\lambda = \lambda^{max} . T_C . g_N^* / (g_E^* + g_N^*). \quad (\text{A.11})$$

These expressions have a simple and logical interpretation. The rates  $g_E^*$  and  $g_N^*$  are the potential specific phytoplankton growth rates determined by light and nutrient separately, and we can think of them as measures of light and nutrient availability as perceived by the cell. The achieved growth rate  $g$  is a compromise between the two. If one is much larger than the other, then the achieved growth rate is very close to the smaller rate. Note that simple non-adaptive models of phytoplankton growth often multiply a light-limitation and a nutrient-limitation term. It is well known that this underestimates growth rates. Our approach partly avoids the defect of multiplicative growth models. In (A.9), the nitrogen:carbon ratio approaches  $\chi^{min}$  when light is much more available than nutrient ( $g_E^* \gg g_N^*$ ), and it approaches  $\chi^{max}$  when  $g_N^* \gg g_E^*$ , as one might expect. The chlorophyll-a:carbon ratio,  $\lambda$ , approaches  $\lambda^{max}$  when light is limiting and nutrient is abundant ( $g_N^* \gg g_E^*$ ), and it approaches zero when nutrient is strongly limiting and light is saturating.

It is possible to treat  $g_N$  as an  $N$ -specific uptake rate, and for the maximum specific uptake rate of nitrogen ( $V^{max}$ ) to be substantially larger than the maximum  $C$ -specific growth rate ( $g^{max}$ ). This would allow rapid uptake of nitrogen in a dynamic quota model.

However, given that we are considering only balanced growth here, we treat  $g_N$  as a specific growth rate and assume  $V^{max} = g^{max}$ . We must then interpret  $K$  as a half-saturation constant for growth rather than uptake:

$$K = \frac{g^{max} . T_C}{a_N}. \quad (\text{A.12})$$

64 With this simplification (substitute (A.12) into the  $N/(K + N)$  term of (A.8)), we can  
 65 write:

$$h_N = N/((g^{max}.Tc/a_N) + N), \quad (\text{A.13})$$

66 and from (A.7) we set

$$h_E = 1 - \exp(-\alpha.\lambda^{max}.E/g^{max}). \quad (\text{A.14})$$

67 As before, under the assumption of balanced growth ( $g = g_C = g_N$ ), we obtain

$$g = Tc.g^{max}.h_E.h_N/(h_E + h_N), \quad (\text{A.15})$$

68 and

$$\chi = (h_E.\chi^{min} + h_N.\chi^{max})/(h_E + h_N). \quad (\text{A.16})$$

69 If we set  $R_N = \chi^{min}/\chi^{max}$ , then

$$\chi = \chi^{max}.(h_E.R_N + h_N)/(h_E + h_N), \quad (\text{A.17})$$

70 and

$$\lambda = \lambda^{max}.Tc.h_N/(h_E + h_N). \quad (\text{A.18})$$

71 The phytoplankton chlorophyll-a:nitrogen ratio equals  $\lambda/\chi$ , and it is given by:

$$Chla : N = (\lambda^{max}.Tc/\chi^{max}).h_N/(h_E.R_N + h_N). \quad (A.19)$$

## A.2 The transport operator

In this section we describe the transport operator,  $\mathbf{T}(\mathbf{c}, \mathbf{x}, t)$ , used in equation (5) in the main text. The specific form applied to each of the state variables differs based on the characteristics of the specific state variable being operated on.

The change in mixed layer depth ( $MLD$ ) is given by:

$$\psi(t) = \frac{d(MLD)}{dt}, \quad (A.20)$$

and we define

$$\psi^+(t) \equiv \max\{\psi(t), 0\}. \quad (A.21)$$

This form of exchange across the mixed-layer has been adopted from Evans and Parslow (1985). Therefore the state equations, including the effects of changes in the mixed layer, can be written as:

$$\frac{dP}{dt} = g \cdot P - gr \cdot Z + \frac{\kappa + \psi^+(t)}{MLD} \cdot (BCP - P), \quad (A.22)$$

$$\frac{dZ}{dt} = E_Z \cdot gr \cdot Z - m \cdot Z + \frac{\psi(t)}{MLD} \cdot (BCZ - Z), \quad (A.23)$$

$$\frac{dD}{dt} = (1 - E_Z) \cdot f_D \cdot gr \cdot Z + m \cdot Z - r \cdot D - S_D \cdot D / MLD + \frac{\kappa + \psi^+(t)}{MLD} \cdot (BCD - D), \quad (\text{A.24})$$

$$\frac{dN}{dt} = -g \cdot P + (1 - E_Z) \cdot (1 - f_D) \cdot gr \cdot Z + r \cdot D + \frac{\kappa + \psi^+(t)}{MLD} \cdot (BCN - N), \quad (\text{A.25})$$

81 where  $\kappa$  is the background mixing,  $S_D$  is the detrital sinking rate (a parameter subject to  
 82 inference), and  $BCP$ ,  $BCZ$ ,  $BCD$  and  $BCN$  are the boundary conditions for  $P$ ,  $Z$ ,  $D$  and  
 83  $N$ , respectively. With the exception of  $BCN$  all other state variable boundary conditions  
 84 are set to 0. It is assumed that as the mixed layer shoals,  $P$ ,  $D$  and  $N$  are lost from the  
 85 mixed layer, whereas  $Z$  is assumed to be retained in the mixed layer. As the mixed layer  
 86 deepens,  $P$ ,  $Z$  and  $D$  concentrations will be diluted, whereas  $N$  will be added in an amount  
 87 proportional to the prescribed boundary condition  $BCN$ . The variables  $\kappa$ ,  $\psi$ ,  $MLD$  and  
 88  $BCN$  are considered to be exogenous forcing and are prescribed.

### 89 **A.3 The light model**

$$E = E_0 \cdot (1 - \exp(-Kz)) / Kz, \quad (\text{A.26})$$

90 where  $E_0$  is the mean daily photosynthetically available radiation (PAR) just below the  
 91 air-sea interface, and  $Kz$  is given by:

$$Kz = (K_W + a_{Ch} \cdot Chla) \cdot MLD. \quad (\text{A.27})$$



92 In (A.27),  $K_W$  is attenuation due to the seawater,  $a_{Ch}$  is attenuation due to *Chla* and  
93  $MLD$  is the mixed layer depth.

## 94 **A.4 The parameter (prior) model**

95 Where possible, the priors for the process-model parameters have been based on  
96 information in the literature. The parameters can be divided into three classes.  
97 For some physiological parameters, there are existing meta-analyses in the literature that  
98 provide estimates of parameter means and variances. Previous studies of phytoplankton by  
99 Tang (1995) and Montagnes et al. (1994), and of zooplankton by Hansen et al. (1997), have  
100 derived allometric relationships (log-log regressions) for phytoplankton and zooplankton  
101 parameters  $g^{max}$ ,  $\lambda^{max}$ ,  $E_Z$ ,  $Cl_Z$  and  $I_Z$  as a function of individual size. From these data  
102 sets, we have derived prior means and coefficients of variation (Table A1), assuming that  
103 the phytoplankton community at OSP is dominated by small cells (mean cell volume 100  
104  $\mu\text{m}^3$ ), and grazing is dominated by microzooplankton (mean individual volume  $10^5\mu\text{m}^3$ ).  
105 We have used normal prior distributions for those parameters having small coefficient of  
106 variation, and log-normal prior distributions for the rest.  
107 For some parameters, we can draw on a range of quoted values in the literature that are  
108 sufficient to provide crude estimates of prior mean and variance. Historical observations of  
109 the light attenuation due to water,  $K_W$ , and the specific absorption coefficient for  
110 chlorophyll-a,  $a_{Ch}$ , were taken from Kirk (1994). The maximum quantum yield is assumed  
111 constant at  $0.1 \text{ mol } C \text{ mol photons}^{-1}$ , or  $1200 \text{ mg } C \text{ mol photons}^{-1}$ . Estimates of the  
112 affinity of phytoplankton for dissolved inorganic nitrogen,  $a_N$ , are based on data in Hein  
113 et al. (1995) and on theoretical calculations of the diffusion limit to uptake.  
114 Other parameters can be regarded as semi-empirical, representing ecosystem properties and

processes that are only crudely represented in the model. We do not model zooplankton respiration explicitly, and we assume that approximately half of the ingested nitrogen that does not appear as an increase in biomass is released as unassimilated fecal pellets, and half is lost through respiration and excretion of dissolved inorganic nitrogen (cf. Parsons and Takahashi, 1973), so  $f_D$  is given a prior mean of 0.5 and a small CV of 0.1 (Table A1). Because zooplankton grazing is assumed to be dominated by micro-zooplankton, we have assigned the detrital sinking rate  $S_D$  a relatively small prior mean of 5 m d<sup>-1</sup>, with a large CV of 1.0.

Detrital organic matter comprises diverse organic compounds that vary widely in their susceptibility to bacterial attack and remineralization. In the model, very labile organic nitrogen compounds such as amino acids, which may be utilized and remineralized on time scales of hours, are treated implicitly as part of the fraction  $(1 - E_Z).(1 - f_D)$  of ingestion that is released directly as dissolved inorganic nitrogen. A mean remineralization rate of 0.1 d<sup>-1</sup> is applied to the remaining detritus, with a relatively large CV of 0.5. The quadratic mortality rate for zooplankton,  $m_Q$ , is an empirical ecosystem parameter, representing the density-dependent predation on micro-zooplankton. It has been assigned a mean value of 0.01 d<sup>-1</sup> (mg N m<sup>-3</sup>)<sup>-1</sup>, corresponding to a mortality rate of 0.1 d<sup>-1</sup> at typical micro-zooplankton biomass levels of 10 mg N m<sup>-3</sup>. Because we have little prior information to constrain  $m_Q$ , we have assigned it a large CV of 1.0.

The scale factors  $PDF$  and  $ZDF$  have been assigned a prior mean of 0.2. This is a relatively low value, and it corresponds to a diverse community in which the community mean properties show substantially less variation than those of individual species (see Appendix B). The prior variance is set to 0.4, so the prior distribution allows higher values of  $PDF$  and  $ZDF$ , and also less diverse communities.

Table A1: The priors on parameters used in the stochastic NPZD model are all log-normal, with mean ( $\mu$ ) and standard deviation ( $\sigma$ ) on the log-scale, except for  $S_D$  which is Gaussian.

Parameter	Description	Mean( $\mu$ )	SD ( $\sigma$ )
$K_W$	Light Attenuation: Water	$0.03 \text{ m}^{-1}$	0.2
$a_{Ch}$	Light Attenuation: Chla	$0.04 \text{ m}^2 \text{ mg Chla}^{-1}$	0.3
$S_D$	Detrital Sinking Rate	$5 \text{ m d}^{-1}$	1.0
$f_D$	Fraction of grazing to detritus	0.5	0.1
$PDF$	Phytoplankton Diversity Factor	0.15	0.4
$ZDF$	Zooplankton Diversity Factor	0.15	0.4
$\mu_{g^{max}}$	Maximum Carbon Specific Growth Rate	$1.2 \text{ d}^{-1}$	0.63
$\mu_{R_N}$	Ratio between $\chi^{min}$ and $\chi^{max}$	0.25	0.3
$\mu_{\chi^{max}}$	Maximum <i>Chla</i> to <i>C</i> ratio	0.03	0.37
$\mu_{a_N}$	Phytoplankton affinity for <i>N</i>	$0.3 \text{ d}^{-1} \text{ mg } N^{-1} \text{ m}^3$	1
$\mu_{I_Z}$	Maximum Zooplankton ingestion rate	$4.7 \text{ d}^{-1}$	0.7
$\mu_{Cl_Z}$	Maximum Zooplankton clearance rate	$0.2 \text{ m}^3 \text{ mg } N^{-1} \text{ d}^{-1}$	1.3
$\mu_{E_Z}$	Zooplankton growth efficiency	0.32	0.25
$\mu_{m_Q}$	Zooplankton quadratic mortality rate	$0.01 \text{ d}^{-1} \text{ mg } N^{-1} \text{ m}^3$	1
$\mu_{r_D}$	Detrital remineralization rate	$0.1 \text{ d}^{-1}$	0.5

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