

Modeling ecosystem disruptive algal blooms: positive feedback mechanisms

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Supplement 1. Nutrient–phytoplankton–zooplankton (NPZ) model

The stoichiometric NPZ model included a limiting nutrient (nitrogen), 3 species of phytoplankton, and a single species of zooplankton. The 3 species of phytoplankton were modeled after the diatoms *Thalassiosira pseudonana* (T.p.) and *T. weissflogii* (T.w.), and the brown tide species *Aureoumbra lagunensis* (A.l.). The zooplankton species was assumed to be a general large ciliate (cell volume 6.9×10^4 to $21 \times 10^4 \mu\text{m}^3$; Hansen et al. 1997). In parameters and equations, phytoplankton were indexed as $i = 1$ for A.l., $i = 2$ for T.p., and $i = 3$ for T.w. All model simulations used the base parameter values listed below unless otherwise stated (see 'Scenarios' section of the table in Supplement 1). Simulations were programmed in R using the deSolve package (R Development Core Team 2011).

Parameters

Name	Description	Base value	Units	Source
N_{in}	Concentration of limiting nutrient (ammonium) in the inflowing water	12	μM	Assumed
δ	Dilution rate of the system	0.1	d^{-1}	Assumed
$V_{\text{max},1}$	Observed maximum nutrient uptake by algal species 1 (A.l.)	0.0636	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$	Supplement 2
a_1	Intercept of nutrient uptake by A.l.	-0.009	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$	Supplement 2
b_1	Slope of nutrient uptake by A.l.	1.597	$\text{l (}\mu\text{mol C)}^{-1} \text{d}^{-1}$	Supplement 2
$\mu'_{\text{max},1}$	Theoretical maximum growth rate of A.l.	0.591	d^{-1}	Supplement 2
$Q_{\text{min},1}$	Minimum nutrient content necessary for positive growth rate of A.l.	0.031	$\text{mol N (mol C)}^{-1}$	Supplement 2
$\mu_{\text{max},1}$	Observed maximum growth rate of A.l.	0.46	d^{-1}	Supplement 2
$V'_{\text{max},2}$	Theoretical maximum nutrient uptake by algal species 2 (T.p.)	0.47	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$	Sunda et al. (2009)

$V_{\max,2}$	Observed maximum nutrient uptake by T.p.	0.193	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$	Sunda et al. (2009)
K_2	Half-saturation constant of nutrient uptake by T.p.	0.140	μM	Sunda et al. (2009)
S_2	Nutrient concentration below which uptake ceases for T.p.	0.005	μM	Sunda et al. (2009)
$\mu'_{\max,2}$	Theoretical maximum growth rate of T.p.	3.68	d^{-1}	Sunda et al. (2009)
$Q_{\min,2}$	Minimum nutrient content necessary for positive growth rate of T.p.	0.082	$\text{mol N (mol C)}^{-1}$	Sunda et al. (2009)
$\mu_{\max,2}$	Observed maximum growth rate of T.p.	1.45	d^{-1}	Sunda et al. (2009)
$V'_{\max,3}$	Theoretical maximum nutrient uptake by algal species 3 (T.w.)	0.53	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$	Sunda et al. (2009)
$V_{\max,3}$	Observed maximum nutrient uptake by T.w.	0.125	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$	Sunda et al. (2009)
K_3	Half-saturation constant of nutrient uptake by T.w.	0.389	μM	Sunda et al. (2009)
S_3	Nutrient concentration below which uptake ceases for T.w.	0.006	μM	Sunda et al. (2009)
$\mu'_{\max,3}$	Theoretical maximum growth rate of T.w.	1.72	d^{-1}	Sunda et al. (2009)
$Q_{\min,3}$	Minimum nutrient content necessary for positive growth rate of T.w.	0.069	$\text{mol N (mol C)}^{-1}$	Sunda et al. (2009)
$\mu_{\max,3}$	Observed maximum growth rate of T.w.	0.87	d^{-1}	Sunda et al. (2009)
Q_z	Constant nutrient content of zooplankton, assuming Redfield ratio of 1:7	0.143	$\text{mol N (mol C)}^{-1}$	Sterner & Elser (2002)
$g_{\max,1}$	Maximum grazing rate on A.l.	0.72	d^{-1}	Assumed
$g_{\max,2}$	Maximum grazing on T.p.	3.6	d^{-1}	Hansen et al. (1997) ^a
$g_{\max,3}$	Maximum grazing on T.w.	1.44	d^{-1}	Assumed
K_z	Half-saturation value for grazing	12.0	$\mu\text{mol C l}^{-1}$	Hansen et al. (1997) ^a
m	Background mortality rate of zooplankton	0.1	d^{-1}	Assumed
ϵ_a	Assimilation efficiency of grazing	0.8	–	Stoecker (1984)
ϵ_g	Growth efficiency of zooplankton	0.5	–	Hansen et al. (1997) ^b
r	Basal respiration rate of zooplankton	0.1	d^{-1}	Fenchel (2004)
P_τ	Threshold phytoplankton concentration below which grazing ceases	2.0	$\mu\text{mol C l}^{-1}$	Gismervik (2005)

Dynamic state variables

N	Nutrient concentration (ammonium)	$\mu\text{mol N l}^{-1}$
Q_i	Nutrient content of phytoplankton i	$\text{mol N (mol C)}^{-1}$
P_i	Carbon concentration of phytoplankton i	$\mu\text{mol C l}^{-1}$
Z	Carbon concentration of zooplankton	$\mu\text{mol C l}^{-1}$

Algal rate equations

V_i	<p>Nitrogen uptake rate by phytoplankton i</p> <p>For A.l.:</p> $V_i = \begin{cases} \min(V_{\max,i}, a_1 + b_1 N) & \text{for } N > -a/b \\ 0 & \text{otherwise} \end{cases}$ <p>For T.p. and T.w. (Sunda et al. 2009):</p> $V_i = \begin{cases} \min(V_{\max,i}, V'_{\max,i} (N - S_i) / (K_i + N - S_i)) & \text{if } N > S_i \\ 0 & \text{otherwise} \end{cases}$	$\text{mol N (mol C)}^{-1} \text{ d}^{-1}$
μ_i	<p>Specific growth of phytoplankton i (Sunda et al. 2009)</p> $\mu_i = \begin{cases} \min(\mu_{\max,i}, \mu'_{\max,i} (Q_i - Q_{\min,i}) / Q_i) & \text{if } Q_i > Q_{\min,i} \\ 0 & \text{otherwise} \end{cases}$	d^{-1}

Zooplankton rate equations

I_i	Specific carbon ingestion rate of phytoplankton i $I_i = \begin{cases} g_{\max,i} (P_T - P_\tau) (P_i/P_T) / (K_z + P_T - P_\tau) & \text{if } P_T > P_\tau \\ 0 & \text{otherwise} \end{cases}$ where $P_T = \sum_j P_j$	d^{-1}
A_N	Carbon-normalized nitrogen assimilated by zooplankton $A_N = \varepsilon_a \sum_i I_i Q_i$	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$
G_C	Specific rate of carbon supply for growth $G_C = \varepsilon_a \sum_i I_i - r$	d^{-1}
G_N	Carbon normalized nitrogen supply for zooplankton growth $G_N = G_C Q_z$	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$
μ_z	Specific growth of zooplankton $\mu_z = \min(\mu_C, \mu_N)$ where $\mu_C = \varepsilon_g G_C$ is carbon limitation on growth and $\mu_N = A_N/Q_z$ is nutrient limitation on growth	d^{-1}

Nutrient recycling rate equations

R_I	Per-carbon recycling of nutrient from zooplankton egestion $R_I = (1 - \varepsilon_a) \sum_i I_i Q_i$	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$
R_E	Per-carbon recycling of nutrient from zooplankton excretion $R_E = \begin{cases} \max(0, (A_N - G_N)) & \text{if } \mu_C < \mu_N \\ 0 & \text{otherwise} \end{cases}$	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$
R_m	Per-carbon recycling of nutrient from zooplankton mortality $R_m = m Q_z$	$\text{mol N (mol C)}^{-1} \text{d}^{-1}$

Differential equations

$\frac{dN}{dt} = \delta(N_{in} - N) - \sum_i V_i P_i + (R_1 + R_E + R_m)Z$
$\frac{dQ_i}{dt} = V_i - \mu_i Q_i$
$\frac{dP_i}{dt} = (\mu_i - \delta)P_i - I_i Z$
$\frac{dZ}{dt} = (\mu_z - m - \delta)Z$

Initial conditions

$Q_1(0) = 0.14$ $Q_2(0) = 0.13$ $Q_3(0) = 0.15$	Initial nutrient N:C ratios of algae; equal to those observed at maximum growth rate	$\text{mol N (mol C)}^{-1}$
$P_i(0) = 0.01/Q_i(0)$	Initial carbon concentration of phytoplankton i	$\mu\text{mol C l}^{-1}$
$Z(0) = 0.001/Q_z$	Initial carbon concentration of zooplankton	$\mu\text{mol C l}^{-1}$
$N(0) =$ $N_{in} - \sum_i P_i(0)Q_i(0) - Z(0)Q_z$	Initial nutrient concentration	$\mu\text{mol N l}^{-1}$

Scenarios

No grazing	$Z(0) = 0.0$
Grazing rate on A.I.	$g_{\max,1} \in [0.036, 1.44]$; $g_{\max,1} = 0.36, 1.08$
Grazing threshold	$P_{\tau} = 0.0, 2.0$ with dilution rate $\delta = 0.35$
Dilution rate	$\delta \in [0.01, 0.6]$; $\delta = 0.05, 0.3$
Nutrient input	$N_{\text{in}} = 4, 36$

^aBased on an average of the 5 largest ciliates from Table 3 in Hansen et al. (1997)

^bEstimated from a maximum specific ingestion rate of 3.6 d^{-1} , a basal respiration of 0.1 d^{-1} , and an average gross growth efficiency for ciliates of 0.39

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Supplement 2. Ammonium uptake and growth of *Aureoumbra lagunensis*

Sunda et al. (2009) modeled relationships among ammonium concentration, cellular ammonium uptake rate, cellular N:C ratio, and specific growth rate for *Thalassiosira weissflogii* and *T. pseudonana*, based largely on data reported by Sunda & Hardison (2007). Those modeling procedures were repeated for *Aureoumbra lagunensis* based on data reported in Sunda & Hardison (2007, 2010). Here we highlight modeling aspects specific to *A. lagunensis*, but refer to Sunda et al. (2009) for the more detailed description of methods.

Sunda et al. (2009) estimated ammonium uptake rate using a modified Michaelis-Menten model. The modifications were 2-fold: at high ammonium concentrations, uptake was capped at its maximum observed rate, and uptake ceased below a finite low concentration. In between, observed uptake rates of *Thalassiosira weissflogii* and *T. pseudonana*, although modeled with the Michaelis-Menten function, increased approximately linearly. For that reason and because we had few observations for *Aureoumbra lagunensis*, we applied a piece-wise linear model (with 3 pieces) to describe uptake rate of *A. lagunensis*. The piece-wise model preserved the modifications of Sunda et al. (2009)

$$V = \begin{cases} \min(V_{\max}, a + bN) & \text{for } N > -a/b \\ 0 & \text{otherwise} \end{cases} \quad (\text{S1})$$

where V is the uptake rate, N is the nutrient (ammonium) concentration, V_{\max} is the maximum observed uptake rate, a is the y -intercept, and b is the slope. The maximum observed uptake rate was $V_{\max} = 0.0636 \text{ mol N (mol C)}^{-1} \text{ d}^{-1}$ (measured at a growth-saturating ammonium concentration, $32 \mu\text{M}$), and parameter estimates were $\hat{a} = -0.009 \text{ mol N}$ and $\hat{b} = 1.597 (\mu\text{mol C})^{-1} \text{ d}^{-1}$ (Fig. S1).

As in Sunda et al. (2009), we modeled the specific growth rate (μ) using the Droop equation (Droop 1968):

$$\mu = \mu'_{\max}(Q - Q_{\min})/Q \quad (\text{S2})$$

where μ'_{\max} is the theoretical maximum uptake rate (essentially an equation-fitting parameter), Q is the cellular N:C ratio, and Q_{\min} is the lower threshold of Q at which the growth rate equals zero. We used nonlinear least squares to estimate parameters, and a bootstrap of residuals ($n = 2000$) to compute standard errors (Sunda et al. 2009). Estimates (standard errors) were $\hat{\mu}'_{\max} = 0.591 (0.007) \text{ d}^{-1}$ and $\hat{Q}_{\min} = 0.031 (0.001) \text{ mol N (mol C)}^{-1}$. Growth was capped at the rate observed under growth-saturating ammonium, $\mu_{\max} = 0.46 \text{ d}^{-1}$ (Fig. 2B in the present paper).

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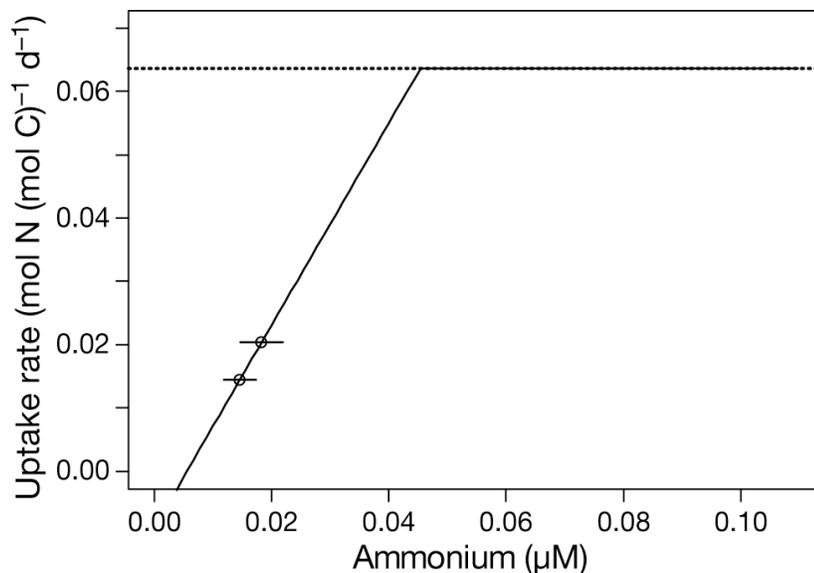


Fig. S1. Modeled relationship for nitrogen uptake rate versus ammonium concentration in *Aureoumbra lagunensis*. Modeled uptake rates were fitted to observed means of replicate observations (circles with standard deviations shown), and were capped at the observed maximum value (dotted horizontal line)

Supplement 3. Effect of varying half-saturation value for grazing

Model simulations in the present paper assumed that the half-saturation value for grazing ($K_z = 12.0 \mu\text{mol C l}^{-1}$) was the same across phytoplankton species (Supplement 1). Simulations here repeated those displayed in Fig. 6 (present paper), but allowed K_z to vary inversely with the maximum grazing rate relative to that of the most palatable species, *Thalassiosira pseudonana*. Thus, K_z equaled $12.0/0.2 = 60.0$ for *Aureoumbra lagunensis*, $12.0/1.0 = 12.0$ for *T. pseudonana*, and $12.0/0.4 = 30.0$ for *T. weissflogii*. Results of these simulations are shown in Fig. S2.

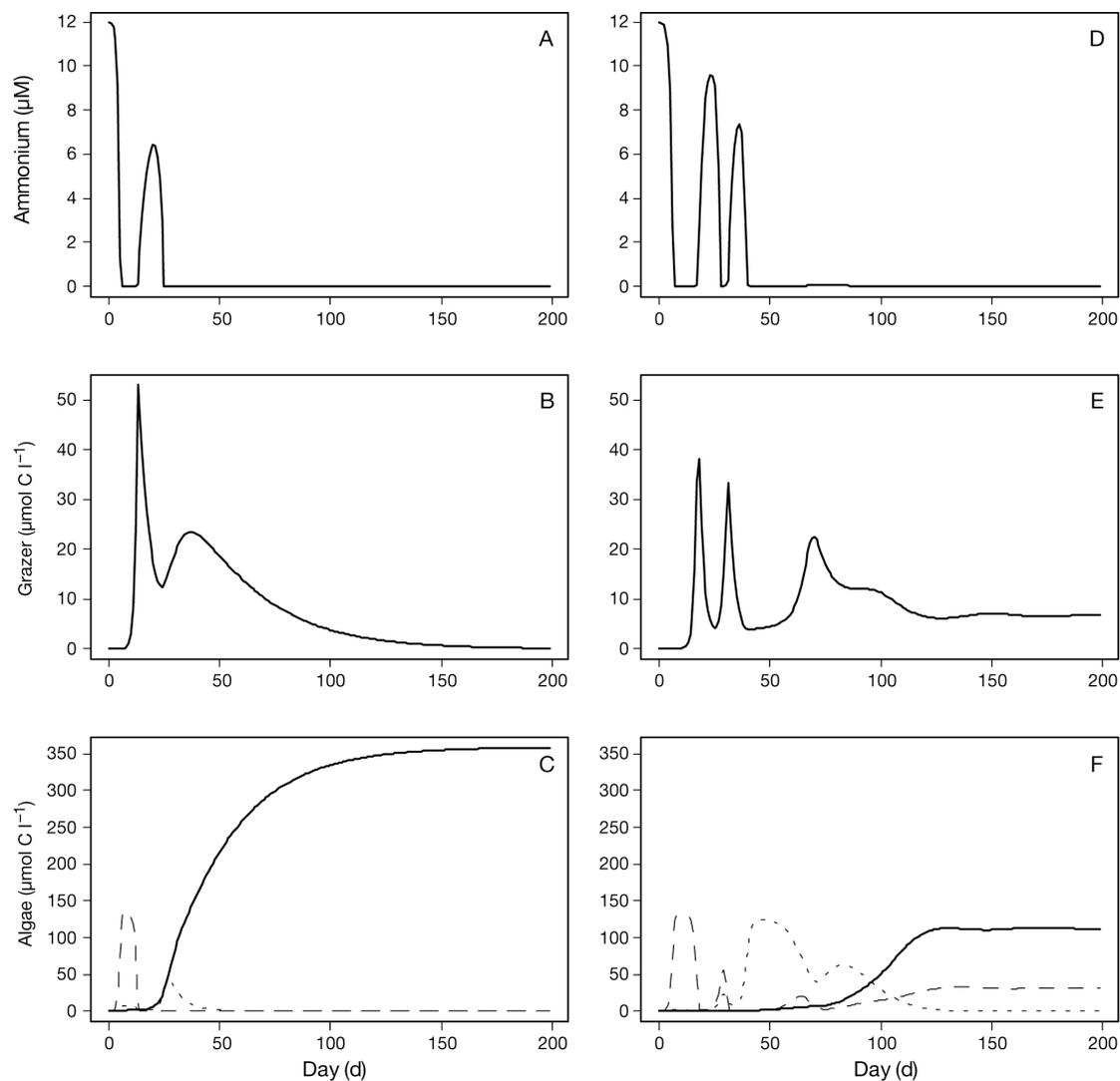


Fig. S2. Two time-course simulations, 1 with dilution rate $\delta = 0.05 \text{ d}^{-1}$ (A, B, C) and 1 with $\delta = 0.30 \text{ d}^{-1}$ (D, E, F). In Panels C and F, the algal species are *Aureoumbra lagunensis* (A.l., solid line), *Thalassiosira pseudonana* (T.p., long-dashed line), and *T. weissflogii* (T.w., short-dashed line). In these simulations, both the half-saturation grazing values and the maximum grazing rates varied among the species as described in Supplement 3