

Eddy-resolving Simulation of Plankton Ecosystem Dynamics in the California Current System - Supplementary Material

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1 Ecosystem Model

For completeness, we repeat here the main equations of the ecosystem model (i.e. equations (2) through (8) of the main text) as well as the table containing the parameter descriptions and values (i.e. Table 1 in the main text):

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$$J(P) = \mu_P^{max}(T, I) \cdot \gamma(N_n, N_r) \cdot P - g_Z^{graz} Z \frac{P}{K_P + P} - \eta_P^{mort} P - k^{coag} P \cdot (P + D_S) \quad (1)$$

$$J(Z) = g_Z^{graz} \beta_Z^{assim} Z \frac{P}{K_P + P} - \eta_Z^{metab} Z - \eta_Z^{mort} Z^2 \quad (2)$$

$$J(N_n) = -\mu_P^{max}(T, I) \cdot \gamma(N_n) \cdot P + k^{nitr}(I) \cdot N_r \quad (3)$$

$$J(N_r) = -\mu_P^{max}(T, I) \cdot \gamma(N_r) \cdot P - k^{nitr}(I) \cdot N_r + \eta_Z^{metab} Z + k_{D_S}^{remin} D_S + k_{D_L}^{remin} D_L \quad (4)$$

$$J(D_S) = g_Z^{graz} \cdot (1 - \beta_Z^{assim}) \cdot (1 - \Omega_Z^{egest}) \cdot Z \frac{P}{K_P + P} + \eta_P^{mort} P + \eta_Z^{mort} \cdot (1 - \Omega_Z^{mort}) Z^2 - k^{coag} D_S \cdot (P + D_S) - k_{D_S}^{remin} D_S \quad (5)$$

$$J(D_L) = g_Z^{graz} \cdot (1 - \beta_Z^{assim}) \Omega_Z^{egest} Z \frac{P}{K_P + P} + \eta_Z^{mort} \Omega_Z^{mort} Z^2 + k^{coag} \cdot (P + D_S)^2 - k_{D_L}^{remin} D_L \quad (6)$$

$$J(\theta) = \mu_P^{max}(T, I) \cdot \gamma(N_n, N_r) \left(\frac{\mu_P^T(T) \cdot \gamma(N_n, N_r) \cdot \theta^{max}}{\sqrt{(\mu_P^T(T))^2 + (\alpha_P I \theta)^2}} - \theta \right) \quad (7)$$

1.1 Phytoplankton

Equations for the parameterization of the growth terms of phytoplankton are given in section 2.2 of the main text. We discuss here only the basis of our choice of the rate constants: We adopt the values of Olivieri and Chavez (2000) for K_{N_n} and K_{N_r} , respectively. Their choice of $K_{N_n} = 0.75 \text{ mmol m}^{-3}$ is slightly higher than the value of 0.5 mmol m^{-3} originally used by Fasham et al. (1990), in order to account for the high concentrations of nitrate and low concentrations of ammonium generally encountered in upwelling regions. These values are also similar to those used in previous coupled circulation/ecosystem model simulations of the CCS (Moisan and Hofmann, 1996; Moisan et al., 1996).

Three processes are responsible for the loss of phytoplankton biomass: zooplankton grazing, coagulation with small detritus, and mortality. The first two processes are described in sections 1.2 and 1.4 below. Phytoplankton mortality, which parameterizes a suite of processes including death by senescence, viral infections, etc. (see e.g. Christian and Anderson (2002)), is parameterized using a linear function with a mortality rate, η_P^{mort} , with the resulting organic matter being allocated to the small detrital pool, D_S . This formulation is similar to that used to model ecosystems in the oligotrophic region of the North Atlantic subtropical gyre near Bermuda (Fasham et al., 1990; Doney et al.,

Table 1

Values, units, and definitions for the parameters of the ecological-biogeochemical model

Parameter	Symbol	Value	Units
<i>Phytoplankton Parameters</i>			
Half-sat. conc. for nitrate uptake	K_{N_n}	0.75	mmol m ⁻³
Half-sat. conc. for ammonium uptake	K_{N_r}	0.50	mmol m ⁻³
Phytoplankton linear mortality rate	η_P^{mort}	0.024	day ⁻¹
Initial slope of P vs I relationship	α_P	1.0	mg C (mg Chla W m ⁻² day) ⁻¹
Max. chlorophyll-a to carbon ratio	θ^{max}	0.0535	mg Chla (mg C) ⁻¹
<i>Zooplankton Parameters</i>			
Zooplankton grazing rate	g_Z^{graz}	0.6	day ⁻¹
Zooplankton assimilation efficiency	β_Z^{assim}	0.75	-
Z.plankt. grazing half-sat. conc. for P	K_P	1.0	mmol N m ⁻³
Zooplankton quadratic mortality rate	η_Z^{mort}	0.1	day ⁻¹ (mmol m ⁻³) ⁻¹
Zooplankton basal metabolism rate	η_Z^{metab}	0.1	day ⁻¹
Zooplankton mortality alloc. fract.	Ω_Z^{mort}	0.33	-
Zooplankton egestion alloc. fract.	Ω_Z^{egest}	0.33	-
<i>Remineralization and Coagulation Parameters</i>			
Nitrification rate in the dark	$k^{nitr,max}$	0.05	day ⁻¹
Nitrification inhibition threshold I	$I_{N_r}^{th}$	0.0095	W m ⁻²
Nitrification inhibition half-dose I	$I_{N_r}^{hd}$	0.036	W m ⁻²
Particle coagulation rate	k^{coag}	0.005	day ⁻¹ (mmol m ⁻³) ⁻¹
Remineralization rate of D_S	$k_{D_S}^{remin}$	0.03	day ⁻¹
Remineralization rate of D_L	$k_{D_L}^{remin}$	0.01	day ⁻¹
Remineralization rate of S_D	$k_{S_D}^{remin}$	0.003	day ⁻¹
<i>Sinking Parameters</i>			
Sinking velocity of P	w_P^{sink}	0.5	m day ⁻¹
Sinking velocity of D_S	$w_{D_S}^{sink}$	1.0	m day ⁻¹
Sinking velocity of D_L	$w_{D_L}^{sink}$	10	m day ⁻¹
<i>Optical Parameters</i>			
Light attenuation coeff. for seawater	κ_{sw}	0.04	m ⁻¹
Chl-a specific light attenuation coeff.	κ_{chla}	0.024	m ⁻¹ (mg Chla m ⁻³) ⁻¹

1996; Spitz et al., 2001), in the subarctic northeastern Pacific Ocean (Signorini et al., 2001), in the tropical Pacific Ocean (Christian et al., 2002), in High-Nutrient-Low Chlorophyll (HNLC) regions (Denman and Peña, 1999) and in the California Current System (CCS) (Moisan and Hofmann, 1996). However, usage of this formulation is not cosmopolitan and phytoplankton mortality terms have even been excluded from a recent model focusing on simulating the coastal upwelling system of Monterey Bay, California (Olivieri and Chavez, 2000). Recognizing that mortality may represent a smaller fraction of the total losses in an upwelling system compared to more oligotrophic conditions, we used a mortality rate, $\eta_P^{mort} = 0.024 \text{ day}^{-1}$, that is about 4 times smaller than that originally used by Fasham et al. (1990).

1.2 Zooplankton

Zooplankton grazing of phytoplankton is modeled using a product of a simple hyperbolic function for food-limitation and a linear zooplankton-specific grazing parameter, g_Z^{graz} . Zooplankton is inefficient in assimilating the grazed phytoplankton, therefore only a fraction, β_Z^{assim} , of the total grazing is assumed to lead to zooplankton growth. This is essentially the same formulation used by Fasham et al. (1990), but simplified due to the occurrence of only one food type, i.e. phytoplankton. The unassimilated fraction, $(1 - \beta_Z^{assim})$, assumed to consist of a combination of fecal pellets and uningested phytoplankton parts, is allocated to the small and large detrital pools. The fraction going to the large detrital pool, primarily fecal pellets, is determined by the parameter Ω_Z^{egest} , assumed to be 0.33. This value is not well constrained by the literature, but corresponds to the value that Lima and Doney (2004) used in their model for the North Atlantic in relatively unproductive regions. The remaining fraction, $(1 - \Omega_Z^{egest})$, goes to the small detrital pool.

The form of the mortality term for zooplankton and other top predators in ecosystem models has been the subject of long debate. Several authors have found that a second-order non-linear mortality term can be successful in dampening any intrinsic non-linear oscillations in model solutions (e.g. Steele and Henderson (1992), and Edwards and Brindley (1999)). Therefore, zooplankton mortality was parameterized in our model using a quadratic mortality term, with a mortality rate η_Z^{mort} . A fraction, Ω_Z^{mort} , of the detrital matter resulting from mortality is allocated to the large detrital pool, with the remainder being allocated to the small detrital pool. We adopted a value of 0.33 for Ω_Z^{mort} , based on Fasham et al.'s [1990] value for the fraction of zooplankton mortality going into their detrital pool.

The $\eta_Z^{resp}Z$ term in the zooplankton equation accounts for energy loss due to basal metabolism. This is a term similar to the loss incurred from mortal-

ity except that the nitrogen loss from respiration loss occurs in the form of ammonium.

1.3 Dynamic Phytoplankton Chlorophyll-a to Carbon Ratio

The derivation of the equation for the dynamic chlorophyll-a to carbon ratio, θ , follows much of the logical considerations presented in Geider et al. (1997). We begin by taking the source-sink term for phytoplankton, $J(P)$, (equation (2) in the main text):

$$J(P) = \mu_P^{max}(T, I) \cdot \gamma(N_n, N_r) \cdot P - g_Z^{graz} Z \frac{P}{K_P + P} - \eta_P^{mort} P - k^{coag} P \cdot (P + D_S) \quad (8)$$

and converting it into an equation for cellular chlorophyll-a with units of mg Chl-a m^{-3} by multiplying the first term on the right hand side (the growth term) with a conversion factor α

$$\alpha = \frac{\mu_P^{max}(T, I) \cdot \gamma(N_n, N_r) \cdot \theta^{max} \cdot r_{C:N}^P \cdot 12 \text{mg C}(\text{mmol C})^{-1}}{\alpha_P I \theta} \quad (9)$$

derived from Geider et al. (1997; equation 4) that estimates the proportion of photosynthate that is used for chlorophyll-a biosynthesis. The symbol $r_{C:N}^P$ is the stoichiometric carbon to nitrogen ratio of phytoplankton, assumed to be constant at 106:16.

The remaining terms for grazing, mortality and coagulation are converted into the correct units of chlorophyll-a by multiplying each term by the present chlorophyll-a to nitrogen ratio in phytoplankton, Chl/P . This gives,

$$J(Chl) = \mu_P^{max}(T, I) \cdot \gamma(N_n, N_r) \cdot P \cdot \alpha - g_Z^{graz} Z \frac{P}{K_P + P} \frac{Chl}{P} - \eta_P^{mort} P \frac{Chl}{P} - k^{coag} P \cdot (P + D_S) \frac{Chl}{P}. \quad (10)$$

The equation for the chlorophyll-a to carbon ratio (mg Chl-a (mg C) $^{-1}$) is written as:

$$\theta = \frac{Chl}{P \cdot r_{C:N}^P \cdot 12 \text{mg C}(\text{mmol C})^{-1}}. \quad (11)$$

Using the chain rule, we can define a partial differential equation for θ that

governs the time and space distribution of this non-conservative scalar,

$$\frac{\partial \theta}{\partial t} = \frac{P \frac{\partial Chl}{\partial t} - Chl \frac{\partial P}{\partial t}}{P^2 \cdot r_{C:N}^P \cdot 12 \text{mg C}(\text{mmol C})^{-1}} \quad (12)$$

The resulting source and sink term, $J(\theta)$ is written as

$$J(\theta) = \mu_P^{max}(T, I) \cdot \gamma(N_n, N_r) \left(\frac{\mu_P^T(T) \cdot \gamma(N_n, N_r) \cdot \theta^{max}}{\sqrt{(\mu_P^T(T))^2 + (\alpha_P I \theta)^2}} - \theta \right) \quad (13)$$

as given in the main text (equation 7).

1.4 Particulate Organic Matter

We consider two size classes of particulate organic matter: A small detritus pool (D_S) assumed to have a mean size of about 10 μm , and a large detritus pool (D_L), which includes particles of size 100 μm and larger. This separation of particulate organic matter into two size classes attempts to reflect the observation that particles in the ocean have a relatively smooth size spectrum, with only particles larger than about 100 μm having sinking velocities fast enough to contribute significantly to the export of organic matter out of the near surface ocean. Recent work by Jackson (2001) demonstrated that the size dependence of particle dynamics can be captured reasonably well with a two size class approach. Our consideration of two size classes gives our model considerably more complexity in this pool than what is generally used in comparable NPZD-type models.

Small detritus particles are formed by mortality of phyto- and zooplankton, and egestion/excretion by zooplankton. Large particles are formed by coagulation of phytoplankton with small detritus particles, and by zooplankton mortality and egestion/excretion. Particle coagulation is modeled as a particle density function that assumes that the probability of particles making contact and coagulating is proportional to the concentration of particles (Stolzenbach and Elimelech, 1994). The resulting term states that the rate of coagulation is proportional to the square of the concentration of available particles, i.e. $k^{coag} \cdot (P + D_S)^2$. Coagulation acts therefore in our model as a second ‘‘mortality’’ term for phytoplankton. This approach is motivated by the observation that diatom blooms are often terminated by massive coagulation events (e.g. Alldredge and Gotschalk (1989); Alldredge et al. (1995)).

Phytoplankton and the two detrital pools sink through the water column with constant settling velocities. However, only the large detrital pool has a settling velocity that is large enough for sinking to play a major role in its dynamics,

i.e. 10 m day^{-1} . In contrast, the small size of phytoplankton cells and small detrital particles gives them sinking velocities that are an order of magnitude smaller, i.e. 0.5 m day^{-1} for phytoplankton and 1 m day^{-1} for small particles. These latter sinking velocities are of similar magnitude to the vertical velocities of the water, so that these two pools generally behave more like dissolved pools than particulate pools.

We use a novel numerical technique for representing vertical advection by sinking. This technique was developed by A. Shchepetkin (pers. comm.) on the basis of parabolic splines and permits a particle profile to sink (advect) through the water column with minimal numerical dispersion.

1.5 Remineralization Processes

In most biogeochemical models to date, the recycling of detrital material back into the nitrate pool is handled implicitly. This is accomplished by the inclusion of a loss term for the detrital pools that is then allocated to the nitrate pool (e.g. Fasham et al. (1990); Doney et al. (1996); Olivieri and Chavez (2000)). We have chosen to model these remineralization processes explicitly by including the processes of ammonification, i.e. the conversion of organic nitrogen to ammonium, and of nitrification, i.e. the conversion of ammonium to nitrate.

Organic nitrogen in both the small and large detrital pools is modeled to remineralize with a first-order reaction to ammonium, with reaction rate constants, $k_{D_S}^{remin}$, and $k_{D_L}^{remin}$, respectively. Ammonium is nitrified back to nitrate with a first-order reaction, taking into account photoinhibition, which prevents ammonium from being oxidized in the euphotic zone. We use the daily averaged PAR, \bar{I} , in order to take into account that photoinhibition is not limited to daylight hours, but rather extends into the night (Olson, 1981). The nitrification rate is given by

$$k^{nitr}(I) = k^{nitr,max} \left(1 - \max \left(0, \frac{\bar{I} - I_{N_r}^{th}}{I_{N_r}^{hd} + \bar{I} - I_{N_r}^{th}} \right) \right) \quad (14)$$

where $I_{N_r}^{th}$ is the threshold PAR for nitrification inhibition and $I_{N_r}^{hd}$ is the half-dose PAR for nitrification inhibition. We have adopted the values of Olson (1981) for these two parameters (see Table 1).

The remineralization rate constants, $k_{D_S}^{remin}$ and $k_{D_L}^{remin}$, are not well constrained in the literature. We have chosen them such that their sum is close to the value of the maximum nitrification rate. Since these remineralization rates are first order and the sinking velocities are constant, the vertical flux of particles is given by an exponential function with a remineralization length scale, $L^{remin} =$

w_D^{sink}/k_D^{remin} . In the case of D_S , the length scale is only 30 m, whereas in the case of D_L , the remineralization length scale is 1000 m, about twice the value of 480 m for unprotected organic carbon found by Armstrong et al. (2002) when analyzing open-ocean sediment trap data. Since our model focuses on the upper ocean, this difference will have little impact on our solutions. Regardless of these uncertainties, the large difference in length scales make it clear that most of the sinking of organic matter into the deeper layers of the model must occur by large detrital particles, since the small detrital particles do not make it far below the euphotic zone. An exception is the export of organic matter out of the euphotic zone by advective and convective processes, which can be quite substantial in a few places (see e.g. Plattner et al. (2005)).

1.6 Sediment Processes

A fraction of the sinking material (mostly large detritus) reaches the sea floor. Observations indicate that only a small fraction of the organic matter rain arriving at the sediment is permanently buried (less than 5% in deep sea sediments, and about 8% on ocean margins (Sarmiento and Gruber, 2006)), and that most organic matter is remineralized to inorganic constituents, which diffuse back into the water column. To represent this process, we added a simple sediment model to the bottom layer of our model. This sediment model keeps track of the total organic nitrogen arriving at the sediment and then remineralizes it with a first-order rate back to ammonium, which then is added to the overlying bottom layer of the model. The sediment model has only one state variable, S_D , with units of mmol N m^{-2} . Its tracer conservation equation, solved at every latitude/longitude point of the model below the lowest layer, is given by,

$$\frac{dS_D}{dt} = w_{D_S}^{sink} D_S \Big|_{z=H} + w_{D_L}^{sink} D_L \Big|_{z=H} + w_P^{sink} P \Big|_{z=H} - k_{S_D}^{remin} S_D \quad (15)$$

where H is the depth of the water-sediment interface. The ammonium flux resulting from $k_{S_D}^{remin} S_D$ is added as a flux boundary condition to the bottom layer. In this model, no long-term burial occurs, but pulses of organic matter arriving at the sediments are slowly returned back to the water column as opposed to being instantaneously remineralized. In a recent review, Soetaert et al. (2000) demonstrated that such a simple sediment model is sufficiently accurate for most applications focusing on water column processes.

2 Boundary conditions

2.1 Heat and freshwater fluxes

The total surface heat flux is applied at the surface, except for the solar short-wave radiation component. The non-solar heat flux is comprised of the observed mean flux and a restoring term toward observed surface ocean temperature, representing a thermal feedback with the atmosphere. The restoring coefficient was derived from bulk formulas (Barnier et al., 1995) and varies from place to place. The contribution of the feedback term to the total heat flux is generally small, but critical to maintain long-term equilibrium solutions. The solar radiation component of the heat flux is permitted to penetrate into the ocean, and we use the optical model presented in section 2.3 without consideration of the absorption by chlorophyll to compute the vertical distribution of the heat deposition resulting from the attenuation of light.

The boundary condition for the freshwater flux is formulated analogously to the non-solar heat flux, i.e. using a combination of the climatological net freshwater flux from COADS (da Silva et al., 1994) and a restoring term that is proportional to the difference between the modeled and climatologically observed surface ocean salinity. This restoring is motivated, in part, by the large uncertainty associated with net freshwater fluxes from COADS, a result of having only sparse direct measurements of evaporation and precipitation. The restoring term for salinity also provides a parameterization of the freshwater contribution by runoff from rivers.

2.2 Surface boundary conditions for biogeochemical variables

The surface boundary conditions for the state variables of the ecological-biogeochemical require the consideration of a “virtual flux” term. This virtual flux represents a dilution/concentration effect, which arises in the real ocean from the net addition or removal of freshwater causing a dilution or concentration of chemical and biological quantities. Since our physical model has a fixed volume, we have to “parameterize” this process using salinity as an indicator of freshwater fluxes. We model this virtual flux for all state variables, B , of the ecological-biogeochemical model, $F_{\text{virt}}(B)$, by tying it to the salt flux $F(S)$, i.e.

$$F_{\text{virt}}(B) = F(S) \frac{\langle B \rangle}{\langle S \rangle} \quad (16)$$

where $\langle B \rangle$, and $\langle S \rangle$ are constants, determined by averaging, at each time step, B and S over the surface layer of the model and over the entire

domain. We note that this parameterization is only applicable for the exchange of freshwater with the atmosphere, i.e. freshwater that has zero concentration of the biogeochemical state variables. This does not apply to freshwater fluxes associated with rivers. This effect is not considered in our model.

2.3 Diurnal cycle of PAR

The model calculates a diurnally varying PAR field using the climatological, monthly mean surface solar radiation estimate, I_{tot} in W m^{-2} , that is used to force the circulation model. In this formulation the amount of PAR at the ocean surface, $I(z = 0)$,

$$I(z = 0) = 0.43 \cdot I_{tot} \cdot \max \left(0, \frac{\pi (a \cdot \cos(2\pi((12 + T_{day})/24.) + b))}{a \cdot \sin(\arccos(-c)) + b \cdot \arccos(-c)} \right), \quad (17)$$

where 0.43 is the fraction of the total solar radiation that is PAR, T_{day} is the local time of day in hours. The symbols a, b, c are defined as $a = \cos \delta \cdot \cos \phi$; $b = \sin \delta \cdot \sin \phi$; $c = \tan \delta \cdot \tan \phi$, where ϕ is the latitude in radians, and δ is the declination in radians. The latter is calculated using the Evans and Parslow (1985) formulation as

$$\delta = -0.406 \cos(2\pi T_{yr}/360.), \quad (18)$$

where T_{yr} is the local day number. Since our ROMS model uses a calendar year with 12 months of 30 days, T_{yr} goes from 0-360. The max function modifies the monthly averaged PAR into a diurnally varying PAR. Its integrated mean taken over an entire day is equal to 1 and guarantees that the daily mean of the time-varying PAR remains equal to the monthly mean value from the climatological forcing data. This function would not be required in simulations where a diurnally varying PAR field was not needed, or if the physical model had diurnal forcing.

2.4 Lateral boundary conditions

As done in Marchesiello et al. (2003), the boundary conditions at the lateral open boundaries are given by a combination of outward advection and radiation and flow-adaptive nudging toward prescribed external conditions (Marchesiello et al., 2001). The monthly climatology of temperature and salinity of Conkright et al. (2002) were used together with COADS winds to estimate climatological values for the geostrophic and Ekman baroclinic velocity components. A level of no motion at 500 m depth was assumed to determine the total velocity. The same monthly climatology was employed for determining the nudging values for temperature and salinity throughout the water column.

For nitrate, the same procedure was applied using the monthly (for depths down to 500 m) and annual (for all depths below 500 m) climatology of Conkright et al. (2002). For chlorophyll, a monthly climatology of surface concentrations was created from SeaWiFS data spanning the time from September 1997 to December 2002. Monthly vertical profiles were then created from these surface concentrations using the algorithm of Morel and Berthon (1989). Their algorithm is based on the analysis of about 4000 vertical profiles of chlorophyll for Case 1 waters. They grouped the profiles into trophic categories (based on surface chlorophyll) and determined equations that describe the vertical profile as a function of the surface chlorophyll concentration only (their equation 6 on p. 1557). A minimum value of $0.005 \text{ mg Chl-a/m}^{-3}$ was used for all grid cells that would have had a lower concentration based on the algorithm. The climatological lateral boundary conditions for phytoplankton were derived from the chlorophyll climatology by applying a conversion factor of $0.5 \text{ mmol N/mg Chl-a}$ for the top seven layers and of $0.3 \text{ mmol N/mg Chl-a}$ for the bottom 13 layers. These conversion factors correspond to the mean chlorophyll-a to carbon ratios modeled in the interior of our domain. Finally, the zooplankton climatology was created by applying a conversion factor of $0.2 \text{ mmol N/mg Chl-a}$ for all layers. This conversion factor also represents a typical value for the ratio of zooplankton to chlorophyll-a in the interior domain. The model solutions in the interior part of our domain are essentially insensitive to the details of the lateral boundary conditions for phytoplankton and zooplankton because the growth rates of these two plankton classes are large enough to quickly reach steady-state with the local forcing in the interior of the domain. The remaining ecosystem-biogeochemical variables (i.e., NH_4 , small and large detritus) were set to zero on the boundaries.

3 Analytical steady-state solutions

In the following, we derive the box model steady-state solutions for the different ecosystem variables. In order to simplify the solutions, we often use scaling arguments to eliminate the less important terms in the balance.

3.1 Phytoplankton

In steady-state, i.e. $J(P) = 0$ in equation (1), the phytoplankton equation implies a balance between growth and the losses from grazing, mortality, and coagulation:

$$\mu_P^{max}(T, I) \cdot \gamma(N_n, N_r) = g_Z^{graz} Z \frac{1}{K_P + P} + \eta_P^{mort} + k^{coag} \cdot (P + D_S) \quad (19)$$

For our parameter choices, the dominant loss term is grazing by zooplankton, except for very low phytoplankton concentrations. We therefore subsequently neglect mortality and coagulation, and solve (19) for P , using also the steady-state equation for zooplankton (see below). This results in a quadratic equation with solution:

$$P^{\text{steady-state}} = \frac{-2\varepsilon + (g_Z^{\text{graz}})^2 \cdot \beta_Z^{\text{assim}} - g_Z^{\text{graz}} \cdot \eta_Z^{\text{metab}} \pm g_Z^{\text{graz}} (\text{Det})^{\frac{1}{2}}}{2\varepsilon/K_P}, \quad (20)$$

with the determinant, Det , given by

$$\text{Det} = -4 \cdot \varepsilon \cdot \beta_Z^{\text{assim}} - 2g_Z^{\text{graz}} \beta_Z^{\text{assim}} \eta_Z^{\text{metab}} + \eta_Z^{\text{metab}} + (g_Z^{\text{graz}} \cdot \beta_Z^{\text{assim}})^2, \quad (21)$$

and where the parameter $\varepsilon = \mu_P^{\text{max}}(T, I) \cdot \gamma(N_n, N_r) \cdot K_P \cdot \eta_Z^{\text{mort}}$ includes the growth parameters.

Analysis of the determinant (21) reveals that only total growth rates, $\mu_P^{\text{max}}(T, I) \cdot \gamma(N_n, N_r)$, smaller than about 0.4 day^{-1} give positive values. This requires that for light saturated conditions and for temperatures typical of the CCS, nutrient concentrations need to be below their half saturation constants in order to give real values for $P^{\text{steady-state}}$. We will show below for the solutions of nitrate and ammonium that this is indeed the case. The analytical determination of the steady-state P value for a given total nitrogen content requires the simultaneous solution of all equations, yielding a high-order polynomial equation, which we do not elaborate on here.

3.2 Zooplankton

The steady-state zooplankton to phytoplankton allocation ratio can be computed by setting $J(Z)$ in (2) to zero, solving the resulting equation for Z and then dividing it by P . This gives

$$(Z/P)^{\text{steady-state}} = \frac{g_Z^{\text{graz}} \beta_Z^{\text{assim}} - \eta_Z^{\text{metab}} \left(\frac{K_P}{P} + 1 \right)}{\eta_Z^{\text{mort}} (K_P + P)} \quad (22)$$

3.3 Detritus

We solve for the steady-state of small detritus by setting $J(D_S)$ in (5) to zero and using the steady-state equation for Z (equation (22)). This gives the

following balance between production of small detritus and its loss:

$$\varepsilon_2 \cdot P^2 = k^{coag} D_S \cdot (P + D_S) + k_{D_S}^{remin} D_S, \quad (23)$$

where the production scales with P^2 , and the loss scales with D_S^2 , and where ε_2 is given by:

$$\begin{aligned} \varepsilon_2 = & g_Z^{graz} (1 - \beta_Z^{assim}) (1 - \Omega_Z^{egest}) \frac{g_Z^{graz} \beta_Z^{assim} - \eta_Z^{metab} \left(\frac{K_P}{P} + 1\right)}{\eta_Z^{mort} (K_P + P)^2} \\ & + \frac{\eta_P^{mort}}{P} + \eta_Z^{mort} \cdot (1 - \Omega_Z^{mort}) \left(\frac{g_Z^{graz} \beta_Z^{assim} - \eta_Z^{metab} \left(\frac{K_P}{P} + 1\right)}{\eta_Z^{mort} (K_P + P)} \right)^2. \end{aligned} \quad (24)$$

Equation (23) is a 2nd order polynomial equation in D_S , which has the solution:

$$D_S^{\text{steady-state}} = -\frac{1}{2 k^{coag}} \left(k^{coag} P + k_{D_S}^{remin} - \left((k^{coag} P + k_{D_S}^{remin})^2 + 4 k^{coag} \varepsilon_2 P^2 \right)^{\frac{1}{2}} \right) \quad (25)$$

where we show only the solution that gives positive values for D_S . Because the remineralization rate constant is much larger than the product of the coagulation rate and phytoplankton, i.e. $k_{D_S}^{remin} \gg k^{coag} \cdot P$, the above equation can be simplified to

$$D_S^{\text{steady-state}} = -\frac{1}{2 k^{coag}} \left(k_{D_S}^{remin} - \left((k_{D_S}^{remin})^2 + 4 k^{coag} \cdot \varepsilon_2 P^2 \right)^{\frac{1}{2}} \right) \quad (26)$$

At moderately low phytoplankton abundances, ε_2 simplifies to η_P^{mort}/P . Furthermore, it turns out that the product $4 \cdot k^{coag} \cdot \eta_P^{mort}$ is about half as large as $(k_{D_S}^{remin})^2$. If we therefore set $4 \cdot k^{coag} \cdot \eta_P^{mort} = 0.5 \cdot (k_{D_S}^{remin})^2$, we can eliminate this term from the square root, leaving only the expression $1 + 0.5 \cdot P$ inside the root. If we further make use of the fact that for small values of x , $\sqrt{1+x}$ can be approximated by $1 + x/2$, equation (26) can be further simplified to

$$(D_S)^{\text{steady-state, low Z}} \approx \frac{k_{D_S}^{remin}}{8 k^{coag}} \cdot P \quad (27)$$

In the case where zooplankton is abundant, i.e. once P is above 0.5 mmol N m⁻³, sloppy feeding and zooplankton mortality become important source terms for small particulate detritus. In these circumstances the term $4 k^{coag} \varepsilon_2 P^2$ becomes substantially larger than $(k_{D_S}^{remin})^2$, so that equation (26) can be ap-

proximated by

$$D_S^{\text{steady-state, high } Z} \approx -\frac{k_{D_S}^{\text{remin}}}{2 k^{\text{coag}}} + \sqrt{\frac{\varepsilon_2}{k^{\text{coag}}}} \cdot P \quad (28)$$

For P concentrations between 0.5 to 2 mmol m⁻³, ε_2 has values between 0.2 and 0.1 day⁻¹ (mmol m⁻³)⁻², making the factor in front of P vary from 6.3 to 4.5, explaining the steep slope of D_S in Figure 19 of the main text.

Because of its substantial sinking rates, the steady-state for large detritus is determined by the balance between net production, $J(D_L)$, and sinking. We approximate the sinking term, $-w^{\text{sink}} \partial D_L / \partial z$, by $w^{\text{sink}} \cdot D_L / h$, where h is the depth of the surface box in our box model configuration ($h = 20$ m). This results in the following balance:

$$w^{\text{sink}} \frac{D_L}{h} = g_Z^{\text{graz}} \cdot (1 - \beta_Z^{\text{assim}}) \cdot \Omega_Z^{\text{egest}} Z \frac{P}{K_P + P} + \eta_Z^{\text{mort}} \Omega_Z^{\text{mort}} Z^2 + k^{\text{coag}} (P + D_S)^2 - k_{D_L}^{\text{remin}} D_L, \quad (29)$$

that is linear in D_L and describes the balance between sinking, sloppy feeding, zooplankton mortality, coagulation, and loss by remineralization. A scaling analysis shows that all terms are of similar magnitude, except remineralization. Solving (29) for D_L/P , and using the steady-state solutions for Z (22) and D_S (26) gives:

$$(D_L/P)^{\text{steady-state}} = \frac{2 k^{\text{coag}} D_S^{\text{steady-state}} + P (\varepsilon_3 + k^{\text{coag}}) + k^{\text{coag}} (D_S^{\text{steady-state}})^2 / P}{k_{D_L}^{\text{remin}} + w^{\text{sink}}/h}, \quad (30)$$

with ε_3 given by

$$\varepsilon_3 = g_Z^{\text{graz}} (1 - \beta_Z^{\text{assim}}) \Omega_Z^{\text{egest}} \frac{g_Z^{\text{graz}} \beta_Z^{\text{assim}} - \eta_Z^{\text{metab}} \left(\frac{K_P}{P} + 1 \right)}{\eta_Z^{\text{mort}} (K_P + P)^2} + \eta_Z^{\text{mort}} \cdot \Omega_Z^{\text{mort}} \left(\frac{g_Z^{\text{graz}} \beta_Z^{\text{assim}} - \eta_Z^{\text{metab}} \left(\frac{K_P}{P} + 1 \right)}{\eta_Z^{\text{mort}} (K_P + P)} \right)^2. \quad (31)$$

3.4 Nitrate

The steady-state for nitrate in the well-lit upper ocean is given by the physical supply balancing phytoplankton uptake, i.e.

$$\nabla \cdot K \nabla N_n - \vec{u} \cdot \nabla_h N_n - w \frac{\partial N_n}{\partial z} = -\mu_P^{max}(T, I) \cdot \frac{N_n}{K_{N_n} + N_n} \frac{K_{N_r}}{K_{N_r} + N_r} \cdot P \quad (32)$$

since nitrification is light inhibited. The primary supply pathway is vertical advection, so that the left hand side of equation (32) can be simplified to $-w \frac{\partial N_n}{\partial z}$. As done in our box model simulations, we approximate this latter term by $-w/h \cdot (N_n^{th} - N_n)$, where N_n^{th} is the nitrate concentration of the thermocline waters. This results in a quadratic equation:

$$w N_n^2 + \left(w K_{N_n} - w N_n^{th} + h \mu_P^{max}(T, I) \frac{K_{N_r}}{K_{N_r} + N_r} P \right) \cdot N_n - w N_n^{th} K_{N_n} = 0. \quad (33)$$

A scaling analysis of (33) shows that the linear term (b , second term on the left hand side) is much larger than either the quadratic term (a , first term) or the constant term (c , third term) resulting in the determinant, $b^2 - 4 \cdot a \cdot c$, of this quadratic equation being closely approximated by b^2 . As a consequence, the non-negative solution to (33) is approximately zero:

$$N_n^{\text{steady state}} \approx 0 \ll K_{N_n}. \quad (34)$$

In the 3-D solutions, nitrate remains very high in the nearshore regions, i.e. $N_n \gg K_{N_n}$, while ammonium attains moderate levels. In such a case, the right hand side of the nitrate balance (32) simplifies to $-\mu_P^{max}(T, I) \cdot P$. If we consider the vertical 1-D balance,

$$-w \frac{\partial N_n}{\partial z} = -\mu_P^{max}(T, I) \cdot P \quad (35)$$

and replace the upwelling term on the left hand side again with $-w/h \cdot (N_n^{th} - N_n)$, we arrive at the dynamical 3-D solution:

$$N_n^{\text{steady-state,3D}} = N_n^{th} - \frac{h}{w} \mu_P^{max}(T, I) \cdot P. \quad (36)$$

In the euphotic zone, the steady-state for ammonium is given by the balance between the consumption by phytoplankton uptake and the production from zooplankton metabolism, and the remineralization of small and large detrital particles, i.e.

$$\mu_P^{max}(T, I) \cdot \frac{N_r}{K_{N_r} + N_r} \cdot P = \eta_Z^{metab} Z + k_{D_S}^{remin} D_S + k_{D_L}^{remin} D_L \quad (37)$$

Using the steady-state solutions for Z , D_S , and D_L , the solution to this equation

$$N_r^{\text{steady-state}} = \frac{\varepsilon_4 K_{N_r}}{\mu_P^{max}(T, I) P - \varepsilon_4}, \quad (38)$$

where ε_4 is given by

$$\varepsilon_4 = \eta_Z^{metab} Z^{\text{steady-state}} + k_{D_S}^{remin} D_S^{\text{steady-state}} + k_{D_L}^{remin} D_L^{\text{steady-state}} \quad (39)$$

With our parameter choices, ε_4 scales approximately as $0.2 \cdot P$. This factor is about one order of magnitude smaller than $\mu_P^{max}(T, I)$, so that the steady-state solution of ammonium (38) can be approximated by:

$$N_r^{\text{steady-state}} \approx 0.1 \cdot K_{N_r}. \quad (40)$$

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