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Bacterial Community should be Considered in Ecosystem Model in the Ocean?—Comparison between Community-Based Model, Black Box Model, and Exponential Decay Model

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Abstract—In order to elucidate the appropriate levels of microbial complexity in ecosystem models, I compared the behaviors of community-based model including microbial diversity and simpler models, focusing on particulate and dissolved organic carbon (POC and DOC) in the surface ocean. The ratio of bacteria-mediated POC decay rate and that of DOC decay rate in simpler models to those in the community-based model ranged between 56% and 282%, and between 50% and 2872%, respectively. However, these differences in bacterial functions resulted in much smaller variations in carbon fluxes; the ratio ranged between 77% and 128%. These damped impacts on carbon fluxes were due to the presence of competing processes in POC and DOC decay, i.e., zooplankton grazing and photochemical degradation. These results may undermine the importance of the consideration of microbial diversity in ecosystem models. The model comparison also indicates that the discrimination of free-living bacteria from particle-associated bacteria is important even without considering microbial diversity for simulating carbon fluxes in the surface oceans.

Keywords: microbial diversity, ecosystem functions, carbon cycling

INTRODUCTION

Ecosystem models have improved our understanding of mechanisms to control fluxes of particulate organic carbon (POC) and dissolved organic carbon (DOC) in the surface oceans. Despite recent discovery of high phylogenetic and functional diversity of heterotrophic bacteria (Venter *et al*., 2004), most of ecosystem models parametarize the remineralization process as the first order kinetics of POC or DOC concentration (i.e., "exponential decay" model, see Sarmiento and Gruber, 2006) or as the rate that increases linearly with the total biomass of heterotophic bacteria (i.e., "black-box model" Laws *et al*., 2000). Some models address the importance of bacterial diversity and community structure in regulating carbon fluxes (Miki *et al*., 2008, 2009). However, the quantitative comparison between community-based models and simpler parameterizations (exponential decay models and black-box models) are yet to be done.

In this article, I develop simple ecosystem models for the surface oceans with different complexity in microbial components. I aim to compare the temporal dynamics of ecosystem in response to phytoplankton bloom among four models: (1) community-based model, (2) black box model 1, (3) black box model 2, and (4) exponential decay model. In the community-based model, I assume a minimum level of microbial diversity, only including two functional groups of bacteria: DOC specialists and POC specialists. In this model, the specific decay rates of POC and DOC are flexible through possible change in community structure (i.e., the ratio of DOC specialists and POC specialists). In the black box model 1, I assume a single population of bacteria that consists of both of the free-living cells consuming DOC and particle-associated ones consuming POC. In this model, the flexibility of bacterial functions is achieved by changes in the ratio of free-living cells and particle-associated ones. In the black box model 2, I assume a single component of bacteria that represents total abundance of bacteria, without distinguishing free-living and particle-associated fractions of bacteria. In this model, changes in total abundance of bacteria can alter POC and DOC decay rates. In the exponential decay model, I assume that specific rate of decay of POC and DOC are constant over time.

Through quantitative comparison of these four ecosystem models with different flexibility in POC and DOC consumption rate, I will discuss if consideration of microbial diversity is important or not.

MATERIALS AND METHODS

Model description

Community-Based model

I focused on the dynamics of POC and DOC supplied from phytoplankton (C_P, C_D), and POC generated through zooplankton grazing (C_{PZ}). I defined "aggregates" (A_P) as POC with attached cells of POC specialists (see also Miki and Yamamura, 2005). I also defined free-living cells of POC specialists (F_P) and those of DOC specialists (F_D). I assumed generalist bacterivorous protozoa such as heterotrophic nanoflagellates (H) on free-living cells of POC specialists and DOC specialists and mesozooplankton such as copepods (Z) grazing on particles (C_P and A_P). The units of variables are 10^9 cells or particles per m^3 for A_P, F_P, F_D, H, and Z and mg C per m^3 for C_P, C_{PZ}, and C_D.

Aggregates increase with the colonization of free-living cells of POC specialists to POC at a rate $a_P \cdot (C_P/q_P) \cdot F_P$ where a_P and q_P are clearance rate and carbon content per particle, respectively, noting that the abundance (density) of particles (C_P/q_P) is needed to calculate the colonization rate of bacteria to particles. Aggregates decrease with hydrolysis, vertical sinking and zooplankton grazing. The dynamics is given by,

$$dA_P / dt = a_P \cdot \left(C_P / q_P\right) \cdot F_P - h \cdot A_P - m_V \cdot A_P - g_Z \cdot A_P \cdot Z,$$

where h is the hydrolysis rate, m_V is the constant sinking rate, and g_Z is the clearance rate of mesozooplankton.

Free-living cells of POC specialists increase with production during hydrolysis of aggregates at a rate $e_B \cdot f_F \cdot (q_P/q_B) \cdot h \cdot A_P$ where e_B, f_F and q_B is bacterial growth efficiency, the fraction with which hydrolyzed particles is consumed by bacteria, and bacterial carbon content, respectively. The free-living cells decrease with colonization to POC and protozoan grazing. The dynamics is given by,

$$dF_P / dt = \left(1 + e_B \cdot f_F \cdot q_P / q_B\right) \cdot h \cdot A_P - a_P \cdot \left(C_P / q_P\right) \cdot F_P - g_H \cdot F_P \cdot H,$$

where g_H is the clearance rate of protozoa.

The free-living cells of DOC specialists increase with DOC consumption with clearance rate u_D and decrease with protozoan grazing. The dynamics is given by,

$$dF_D / dt = e_B \cdot u_D \cdot C_D \cdot F_D / q_B - g_H \cdot F_D \cdot H.$$

The abundance of protozoa increases with grazing on bacteria and decreases with natural mortality and predation by higher trophic levels. The dynamics of protozoa is given by,

$$dH / dt = e_H \cdot \left(q_B / q_H\right) \cdot g_H \cdot \left(F_P + F_D\right) \cdot H - \left(m_{H0} + m_H \cdot H\right) \cdot H,$$

where e_H and q_H are growth efficiency and carbon content of protozoa, respectively. The predation by higher trophic levels is parameterized as density-dependent mortality ($m_H H$), based on the assumption that the abundance of predator is proportional to H whereas m_{H0} is per capita density-independent natural mortality.

For mesozooplantkon, I assumed a supply from resting eggs as a very small rate I_Z (2.0 [ind m^{-3} day^{-1}]) because I considered the situation where zooplankton cannot maintain its population before the phytoplankton bloom without this supply but it increases population size during the bloom. The zooplankton increases with consumption of particles and decreases with natural mortality and predation. The dynamics of zooplankton is given by,

$$dZ / dt = I_Z + e_Z \cdot \left(1 / q_Z\right) \cdot g_Z \cdot \left(C_P + \left(q_B + q_P\right) \cdot A_P\right) \cdot Z - \left(m_{Z0} + m_Z \cdot Z\right) \cdot Z,$$

where e_Z, m_{Z0} and $m_Z Z$ are carbon-based growth efficiency, density-independent natural mortality and density-dependent mortality caused by higher trophic levels, respectively.

POC and DOC are supplied from phytoplankton community with a rate s_P and s_D, respectively. These organic carbons decrease with bacterial consumption and mesozooplankton grazing, but are in turn regenerated during grazing on bacteria and particles by mesozooplankton and grazing on bacteria by protozoa;

I calculated these regeneration rates using parameters $r_{Z\to C_P}$, $r_{Z\to C_{PZ}}$ and $r_{Z\to C_D}$. I assumed that a fraction of regenerated POC by mesozooplankton has different physicochemical structures from fresh POC supplied by phytoplankton and that this fraction is not consumed by bacteria and sink at a rate m_{PZ}, which is faster than the sinking rate of fresh POC (m_V). I also assumed that DOC is converted to non-labile carbon that are not consumed by bacteria with a constant rate m_D due to unspecified processes such as photochemical degradation. The dynamics of these fractions are given by,

$$dC_P / dt = s_P\left(PP(t)\right) - a_P \cdot C_P \cdot F_P - m_V \cdot C_P - g_Z \cdot C_P \cdot Z + r_{Z\to C_P} \cdot g_Z \cdot \left(C_P + \left(q_B + q_P\right) \cdot A_P\right) \cdot Z,$$

$$dC_{PZ} / dt = r_{Z\to C_{PZ}} \cdot g_Z \cdot \left(C_P + \left(q_B + q_P\right) \cdot A_P\right) \cdot Z - m_{PZ} \cdot C_{PZ},$$

$$dC_D / dt = s_D\left(PP(t)\right) + \left(1 - f_F\right) \cdot q_P \cdot h \cdot A_P - u_D \cdot C_D \cdot F_D - m_D \cdot C_D + r_{H\to C_D} \cdot q_B \cdot g_H \cdot \left(F_P + F_D\right) \cdot H.$$

In order to avoid using additional differential equations for representing phytoplankton community dynamics, I used a mechanistic model that links total primary production (PP) and supply of POC (s_P) and DOC (s_D) (Dunne *et al.*, 2005; see also Miki *et al.*, 2009),

$$s_P\left(PP(t)\right) = \frac{2 \cdot f_S - f_L + f_L \cdot \sqrt{1 + 8 \cdot PP(t) / PP_0}}{1 + \sqrt{1 + 8 \cdot PP(t) / PP_0}} \cdot PP(t),$$

$$s_D\left(PP(t)\right) = PP(t) - s_P\left(PP(t)\right),$$

where $f_S = 0.14$, $f_L = 0.74$, and $PP_0 = 8.88$ [mg C m^{-3} d^{-1}].

For a simple simulation of phytoplankton bloom, I set $PP(t)$ as follows;

$$PP(t) = \begin{cases} 2.0 & \text{if } t < 0 \quad \text{before the bloom} \\ 2.0 + 1.0 \cdot t & \text{if } 0 \le t \le 20 \quad \text{during the bloom (growing phase)} \\ 22.0 - 2.0 \cdot (t - 20) & \text{if } 20 < t \le 30 \quad \text{during the bloom (decaying phase)} \\ 2.0 & \text{if } t > 30 \quad \text{after the bloom} \end{cases}$$

where the unit of t and $PP(t)$ is d and mg C m^{-3} d^{-1}, respectively.

Black box model 1

Most of assumptions are shared with the community-based model, but I considered a single generalist ecotype only; free-living cells of this group (F_G) consume DOC and colonize to POC and forming aggregates (A_G). The dynamics are given by,

$$dA_G / dt = a_G \cdot \left(C_P / q_P\right) \cdot F_G - h \cdot A_G - m_V \cdot A_G - g_Z \cdot A_G \cdot Z,$$

$$\begin{aligned} dF_G / dt = &\left(1 + e_B \cdot f_F \cdot q_P / q_B\right) \cdot h \cdot A_G + e_B \cdot u_G \cdot C_D \cdot F_G / q_B \\ &- a_G \cdot \left(C_P / q_P\right) \cdot F_G - g_H \cdot F_G \cdot H, \end{aligned}$$

$$dH / dt = e_H \cdot \left(q_B / q_H\right) \cdot g_H \cdot F_G \cdot H - \left(m_{H0} + m_H \cdot H\right) \cdot H,$$

$$dZ / dt = I_Z + e_Z \cdot \left(1 / q_Z\right) \cdot g_Z \cdot \left(C_P + \left(q_B + q_P\right) \cdot A_G\right) \cdot Z - \left(m_{Z0} + m_Z \cdot Z\right) \cdot Z,$$

$$\begin{aligned} dC_P / dt = &s_P\left(PP(t)\right) - a_G \cdot C_P \cdot F_G - m_V \cdot C_P - g_Z \cdot C_P \cdot Z \\ &+ r_{Z \to C_P} \cdot g_Z \cdot \left(C_P + \left(q_B + q_P\right) \cdot A_G\right) \cdot Z, \end{aligned}$$

$$dC_{PZ} / dt = r_{Z \to C_{PZ}} \cdot g_Z \cdot \left(C_P + \left(q_B + q_P\right) \cdot A_G\right) \cdot Z - m_{PZ} \cdot C_{PZ},$$

$$\begin{aligned} dC_D / dt = &s_D\left(PP(t)\right) + \left(1 - f_F\right) \cdot q_P \cdot h \cdot A_G - u_G \cdot C_D \cdot F_G - m_D \cdot C_D \\ &+ r_{H \to C_D} \cdot q_B \cdot g_H \cdot F_G \cdot H. \end{aligned}$$

Black box model 2

The difference from the black box model 1 is that I did not distinguish free-living and particle-attached cells and also did not distinguish POC and aggregates. The dynamics of bacterial abundance (B) is given by,

$$dB / dt = e_B \cdot \left(f_F \cdot v_B \cdot C_P + u_B \cdot C_D\right) \cdot B / q_B - g_H \cdot B \cdot H,$$

where v_B and u_B are the clearance rate of bacteria for POC and DOC. The dynamics of other components are given by,

$$dH / dt = e_H \cdot \left(q_B + q_H\right) \cdot g_H \cdot B \cdot H - \left(m_{H0} + m_H \cdot H\right) \cdot H,$$

$$dZ / dt = I_Z + e_Z \cdot \left(1 / q_Z\right) \cdot g_Z \cdot C_P \cdot Z - \left(m_{Z0} + m_Z \cdot Z\right) \cdot Z,$$

$$dC_P / dt = s_P\left(PP(t)\right) - v_B \cdot C_P \cdot B - m_V \cdot C_P - g_Z \cdot C_P \cdot Z + r_{Z\to C_P} \cdot g_Z \cdot C_P \cdot Z,$$

$$dC_{PZ} / dt = r_{Z\to C_{PZ}} \cdot g_Z \cdot C_P \cdot Z - m_{PZ} \cdot C_{PZ},$$

$$dC_D / dt = s_D\left(PP(t)\right) + \left(1 - f_F\right) \cdot v_B \cdot C_P \cdot B - u_B \cdot C_D \cdot B - m_D \cdot C_D + r_{H\to C_D} \cdot q_B \cdot g_H \cdot B \cdot H.$$

Exponential decay model

In this framework, I only considered the population dynamics of mesozooplankton and assumed that decay rates of POC ($k_{POC,B}$) and DOC ($k_{DOC,B}$) are constant, respectively. The dynamics of the system are given by,

$$dZ / dt = I_Z + e_Z \cdot \left(1 / q_Z\right) \cdot g_Z \cdot C_P \cdot Z - \left(m_{Z0} + m_Z \cdot Z\right) \cdot Z,$$

$$dC_P / dt = s_P\left(PP(t)\right) - k_{POC,B} \cdot C_P - m_V \cdot C_P - g_Z \cdot C_P \cdot Z + r_{Z\to C_P} \cdot g_Z \cdot C_P \cdot Z,$$

$$dC_{PZ} / dt = r_{Z\to C_{PZ}} \cdot g_Z \cdot C_P \cdot Z - m_{PZ} \cdot C_{PZ},$$

$$dC_D / dt = s_D\left(PP(t)\right) + \left(1 - f_F\right) \cdot k_{POC,B} \cdot C_P - k_{DOC,B} \cdot C_D - m_D \cdot C_D + r_{H\to C_D} \cdot q_B \cdot g_H \cdot B \cdot H.$$

Numerical analysis

I determined model-specific parameters and initial conditions in black box model 1 and 2 and exponential decay model by using the information of the equilibrium state before the phytoplankton bloom, which was simulated by the community based model. Let (A_P*, F_P*, F_D*, H*, Z*, C_P*, C_{PZ}*, C_D*) denote the equilibrium value of each component in the ecosystem before the bloom ($t < 0$), which can be obtained long-term numerical integration of differential equations.

For the black box model 1, I set the initial conditions as ($A_G(0)$, $F_G(0)$, $H(0)$, $Z(0)$, $C_P(0)$, $C_{PZ}(0)$, $C_D(0)$) = (A_P*, F_P* + F_D*, H*, Z*, C_P*, C_{PZ}*, C_D*). In order to keep the same carbon flux from DOC to bacteria and the same rate of bacterial colonization to POC at $t = 0$ in the black box model 1 as those at the equilibrium of the community-based model, I determined model-specific parameters (u_G and a_G) to satisfy $u_G \cdot C_D(0) \cdot F_G(0) = u_D \cdot C_D^* \cdot F_D^*$ and $a_G \cdot C_P(0) \cdot F_G(0) = a_P \cdot C_P^* \cdot F_P^*$.

For the black box model 2, I set the initial conditions as ($B(0)$, $H(0)$, $Z(0)$, $C_P(0)$, $C_{PZ}(0)$, $C_D(0)$) = (F_P* + F_D*, H*, Z*, C_P* + A_P*(q_P + q_B), C_{PZ}*, C_D*). I determined v_B and u_B to keep the same carbon fluxes from POC and DOC to bacteria by using $v_B \cdot C_P(0) \cdot B(0) = h \cdot A_P^*$ and $u_B \cdot C_D(0) \cdot B(0) = u_D \cdot C_D^* \cdot F_D^*$.

For the exponential decay model, I set the initial conditions as ($Z(0)$, $C_P(0)$,

$C_{PZ}(0)$, $C_D(0)$) = (Z^*, $C_P^* + A_P^*(q_P + q_B)$, C_{PZ}^*, C_D^*). I determined $k_{POC,B}$ and $k_{DOC,B}$ to keep the same carbon fluxes from POC and DOC to bacteria by using $k_{POC,B} \cdot C_P(0) = h \cdot A_P^*$ and $k_{DOC,B} \cdot C_D(0) = u_D \cdot C_D^* \cdot F_D^*$.

With the above setting, I can prepare almost the same characteristics of ecosystem before the phytoplankton bloom ($t < 0$) in three simpler models as those in the community-based model. Thus, I can focus on the differences in model behaviors only after the simulated occurrence of the phytoplankton bloom ($t > 0$).

RESULTS AND DISCUSSION

Responses of ecosystem to phytoplankton bloom in the community-based model

After the occurrence of the phytoplankton bloom, the abundance of POC specialists (A_P and F_P) increased whereas that of DOC specialists (F_D) decreased (Fig. 1a). Just before the end of phytoplankton bloom ($25 < t < 30$), DOC specialists increased probably due to the increase of DOC supply not only from phytoplankton but also via hydrolysis of POC. The abundance of protozoa (H) also increased after the phytoplankton bloom (Fig. 1a). Carbon components (C_P, C_{PZ}, and C_D) showed temporal changes in response to phytoplankton bloom (Fig. 1b). Specific decay rates of carbons also showed temporal changes during the bloom (Fig. 1c). Due to the delayed increase of mesozooplankton (Z) compared to the increase of POC specialists (Fig. 1a), the bacterial consumption (or mesozooplankton consumption) had higher contribution to the degradation of POC during the bloom (or after the bloom) (Fig. 1c).

Comparison between four models

The flexibility of bacteria-mediated functions in the model ecosystem was different among four models. The flexibility was evaluated by temporal changes in specific decay rate of POC mediated by bacteria (Fig. 2a) and that of DOC mediated by bacteria (Fig. 2b), which were normalized by values before the bloom. Note that these parameters were kept constant as $k_{POC,B}$ ($\approx$0.0275 day^{-1}) and $k_{DOC,B}$ ($\approx$0.00166 day^{-1}), respectively in the exponential decay model. In the community-based model, POC decay rate changed between 48% and 178% of the value before the bloom whereas DOC decay rate changed between 10% and 201% of the value before the bloom. In the black box model 1, decay rates of POC and DOC changed between 70% and 168%, and between 100% and 263%, respectively. In the black box model 2, those value changes between 100% and 332%, and between 100% and 333%, respectively.

I also calculated the deviations of results in three simpler models from those in the community-based model for each time step ($0 < t < 180$). The deviations of POC decay rate from the community-based model ranged between 69% and 229%, between 100% and 282%, and between 56% and 208%, for the black box model 1, the black box model 2, and the exponential decay model, respectively (Fig. 2c). The deviations of DOC decay rate from the community-base model

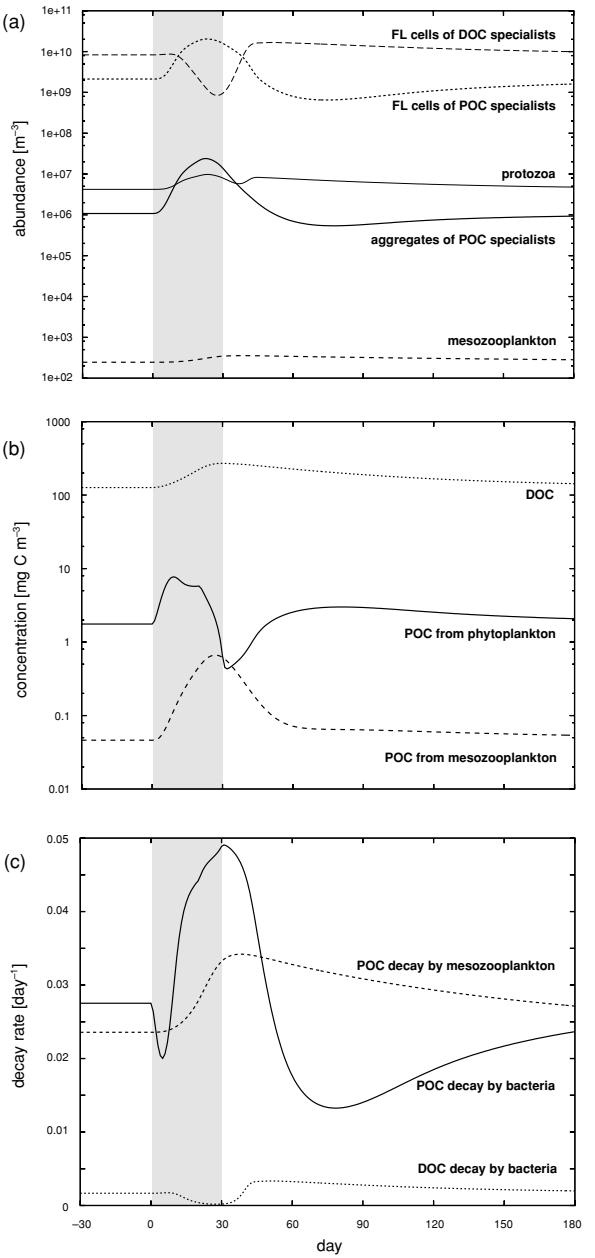

Fig. 1. Ecosystem responses to the phytoplankton bloom. (a) Biological components, (b) organic carbons, and (c) specific decay rate of POC and DOC. Shaded region represents the bloom period. Parameters are $e_B = 0.25$, $e_H = e_Z = 0.5$, $f_F = 0.5$, $r_{Z\to C_P} = r_{Z\to C_{PZ}} = r_{H\to C_D} = 0.1$ (dimensionless), $m_V = 0.1$, $m_{PZ} = 0.2$, $m_{H0} = 0.1$, $m_{Z0} = 0.01$, $m_D = 0.01$ (day^{-1}), $h = 0.05$ (day^{-1}, Sarmiento and Gruber, 2006), $m_H = m_Z = 100$, $a_P = 0.1$, $u_D = 2.0e-4$, $g_H = 100$ (m^3 [10^9 inds.]$^{-1}$ day^{-1}), $g_Z = 9.6e+4$ (m^3 [10^9 inds.]$^{-1}$ day^{-1}, Frost, 1972), $q_B = 0.015$, $q_H = 1000q_B$ (mg C [10^9 cells]$^{-1}$), $q_P = 2000$ (mg C [10^9 cells]$^{-1}$, Frost, 1972), and $q_Z = 1.0e+8$ (mg C [10^9 inds]$^{-1}$, Tande, 1982).

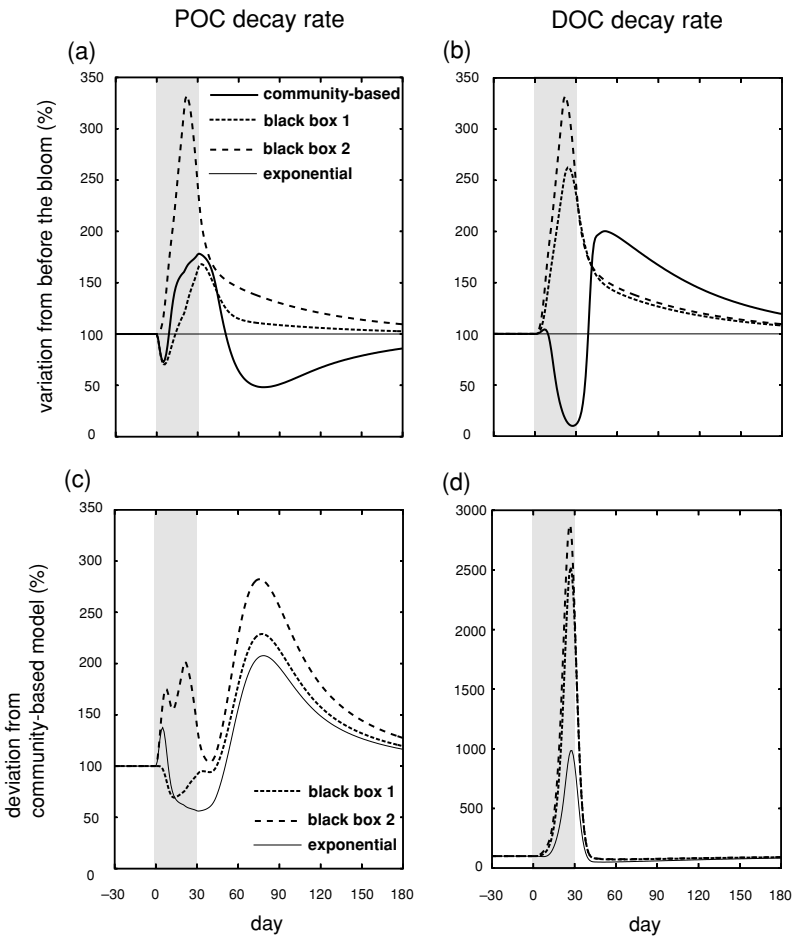

Fig. 2. Flexibility of bacteria functions and variations among models. (a), (b) Variations of specific decay rates (day^{-1}) of POC and DOC after the occurrence of the bloom. (c), (d) Deviation of specific decay rates in simpler models from those in the community-based model.

ranged between 72% and 2522%, between 74% and 2872%, and between 50% and 985%, for three models, respectively (Fig. 2d).

Large variations in bacterial functions (i.e., POC and DOC decay rates) among these four models (Figs. 2c and d) lead to large variations among models in bacterial respiration (Figs. 3a and e). The deviations of results in three simpler models from those in the community-based model ranged between 72% and 253%, between 77% and 268%, and between 52% and 142%, for the black box model 1, the black box model 2, and the exponential decay model, respectively (Fig. 3e). The growth and abundance of mesozooplankton is affected by bacterial activity (indicated by bacterial respiration) through competition for POC. However,

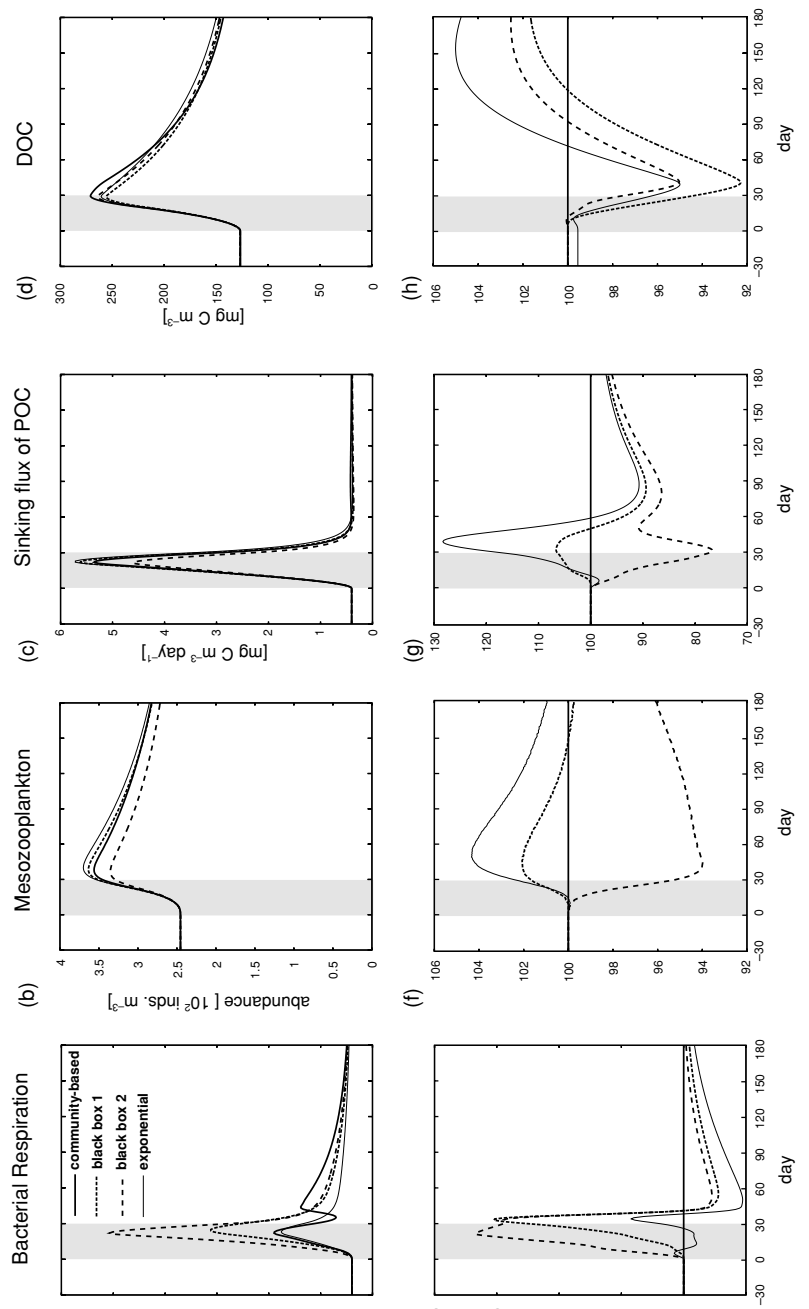

Fig. 3. Model comparisons of ecosystem characteristics. (a)–(d) the absolute value of bacterial respiration, the abundance of mesozooplankton, sinking flux of POC, and DOC concentration. (e)–(h) Deviations of these characteristics in simpler models from those in the community-based model.

variations in mesozooplankton population growth were smaller (Figs. 3b and f). The deviations ranged between 99% and 102%, between 94% and 100%, and between 100% and 104%, for the three simpler models, respectively (Fig. 3f). For the sinking flux of POC (Fig. 3c), the deviations ranged between 89% and 107%, between 77% and 100%, and between 91% and 128%, for the black box model 1, the black box model 2, and the exponential decay model, respectively (Fig. 3g). The deviations in the sinking flux (Fig. 3g) were smaller than those in the bacterial respiration (Fig. 3e) because not only bacteria but also mesozooplankton were consumers of POC and mesozooplankton had higher contribution to POC decay in the later stage of the bloom (Fig. 1c). The deviations in DOC concentration were similarly small (Figs. 3d and h), due to the combined effects of variations in bacterial consumption of DOC and constant loss rate of DOC (m_D = 0.01 day^{-1}) through unspecified processes such as photochemical degradation. The deviations ranged between 92% and 102%, between 95% and 103%, and between 95% and 105%, for the three simpler models, respectively (Fig. 3h), noting that the absolute values can vary depending on the value of m_D.

CONCLUSIONS

The community-based model showed the flexibility of bacterial functions in response to the phytoplankton bloom. This flexibility was well approximated by the black box model 1, but not by the black box model 2 nor the exponential decay model, implying that the discrimination of free-living cells from particle-associated ones is critical parametarization for describing POC and DOC consumption in the surface oceans, rather than the discrimination of POC specialists from DOC specialists. Very large variations in bacteria-mediated DOC decay rate among models imply large space for the improvement of model parameterization for interactions between bacteria and DOC. Despite large differences in the flexibility of bacterial functions and bacterial activity, their impacts on carbon fluxes were smaller. These results indicated that competing processes (e.g., mesozooplankton grazing on POC and photochemical degradation of DOC) could undermine the roles of functional flexibility of bacteria in carbon fluxes in the oceans.

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