Effects of asynchronous fluctuations in DOC supply and bacterial growth on biodegradation efficiency

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Abstract

We present a model of the biodegradation system in which dissolved organic carbon (DOC) is supplied by a continuous flow of wastewater, aerobically decomposed by heterotrophic bacteria, and continuously discharged downstream. In this model, the rate at which DOC is supplied to the system (u) and the maximum growth rate of bacteria (k) fluctuate periodically. We demonstrate analytically how temporal patterns (amplitude, period, and phase difference) in these two fluctuations influence the average DOC concentration and bacterial biomass. These patterns affect: (i) the temporal variability of DOC concentration and (ii) correlations among the fluctuating DOC concentration, the maximum bacterial growth rate, and bacterial biomass. The temporal variability of DOC tends to increase as the relative amplitude of u to k and the fluctuation period increase, leading to a decrease in the average bacterial biomass and biodegradation efficiency. On the other hand, a higher positive (or negative) correlation among fluctuations leads to higher (lower) bacterial biomass and biodegradation efficiency. The sign of the correlations depends on the phase difference between u and k, and tends to be negative at longer periods. The temporal variability of DOC and the effects of correlations among fluctuations determine whether the average DOC concentration is higher or lower than the equilibrium DOC concentration when u and k are temporally constant. Furthermore, the patterns of the fluctuations determine whether the bacterial community is maintained or washed out. In addition, we evaluate numerically the magnitude of the effect of fluctuations. In particular, the dependence on the phase difference can generate a greater than two-fold difference in the average DOC concentration. These results imply that the temporal control of the DOC supply rate, synchronized with the fluctuations of the bacterial community, can improve the efficiency of biodegradation and reduce the DOC concentration in the outflow from a system, even if the total load of DOC delivered to the system is not reduced.
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1. Introduction

One challenge to the effective management of a wastewater treatment system is that posed by temporal fluctuations in the system dynamics; these fluctuations have a great, and mostly negative, impact on the sys-

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tem's performance (e.g., Ahmed et al., 1999). Biological treatment systems are especially vulnerable to fluctuations in temperature and wastewater load content.

The activity in microbial communities, especially heterotrophic bacterial communities, varies temporally in both natural and engineered environments. Temperature is one factor that limits the bacterial growth rate (Morris and Lewis, 1992; Berger et al., 1995; Gurung and Urabe, 1999), abundance (Gurung et al., 2001), and production (White et al., 1991; Unanue et al., 1992; Kirchman and Rich, 1997; Yager and Deming, 1999), and this factor has been well investigated in marine and freshwater ecosystems, and in wastewater treatment systems (Henze et al., 1996; Lishman et al., 2000). Thus, biodegradation rates of organic matter (Cooney et al., 1985; Cronk, 1996) are temperature-dependent and exhibit temporal changes. In addition, the supply rate of pollutants, such as inorganic nutrients or organic carbons, to a biological community changes over time; it depends not only on fluctuating natural conditions, but also on the fluctuating content of anthropogenic loads, such as domestic, municipal, and agricultural wastewater. Domestic and municipal wastewater load content, in turn, is influenced by people's lifestyles (e.g., daily, weekly, and seasonal variations in water use) (Henze et al., 1996); agricultural wastewater load varies with agricultural schedules (Takeda et al., 1997). All of these fluctuations are influenced both by periodic fluctuations, such as seasonal variations, and by non-periodic events, such as temporally flashed loads caused by rain.

In engineered environments, such as bioreactors using activated sludge (suspended-growth processes) or biofilters (attached-growth processes), high concentrations of dissolved oxygen are maintained, whereas dissolved oxygen concentrations vary temporally in natural environments (Miranda et al., 2000; Williams et al., 2000). Furthermore, in engineered environments, flow control regimes, e.g., reactor turnover time and recycle ratio, can buffer the negative effects of temporal variations in pollutant load and can prevent the washout of bacteria, thereby maintaining bacterial activity (Lenas et al., 1994; Ajbar and Gamal, 1997; Ajbar and Ibrahim, 1997; Ajbar and Alhumaizi, 2000). In comparison to engineered systems, it is more difficult to directly control biomass and the production of bacteria in more natural systems, e.g., constructed lagoons and wetlands. Natural systems are more vulnerable to fluctuations in both temperature and wastewater load content. Therefore, it is necessary to investigate the effects of multiple temporal fluctuations on the biodegradation efficiency in these kinds of ecological treatment systems.

Regarding other ecological systems, recent empirical and theoretical studies of food web dynamics have revealed the importance of fluctuating interactions across habitats. These studies show that the relationship between time-varying allochthonous input and autochthonous production critically influences biological communities in situ (Nakano and Murakami, 2001; Takimoto et al., 2002). However, in the context of biodegradation, few studies have focused on the relationship among multiple fluctuations (but see Soetaert et al., 1996). In most modeling studies of the material cycle in natural ecosystems (Billen et al., 1994; Liu et al., 2000; Rittmann et al., 2002), temporal fluctuations have been assumed to be fixed (e.g., temperature, light, and substrate supply concentration). In theoretical and experimental studies of bioreactor systems and oscillating chemostats (Smith, 1981; Lenas et al., 1994; Ajbar and Alhumaizi, 2000), only the fluctuation of the supply rate (i.e., the periodic flow rate of wastewater through reactors or fluctuating supply concentration) has been considered as an important factor determining the system dynamics and a control function for optimization. Bacterial growth depends on the carbon substrate concentration but this growth has not been regarded as being influenced by other potentially fluctuating factors. Therefore, this would be the first study to show theoretically how multiple temporal fluctuations (supply rate and consumption rate) interactively influence the dynamics of a biodegradation system, and to estimate quantitatively their impact on the purification efficiency of the system. We focus on the interaction between the fluctuations in the pollutant load and biological community, and the potentially asynchronous relationship between them. With a fluctuating pollutant load and a time-varying biological community, the relationship between the fluctuations of pollutant supply rate and consumption rate would determine the efficiency of the purification. Roughly speaking, the efficiency would depend on whether the pollutant load fluctuates in phase or out of phase with the changes in biodegradation rates.

In this simple model of the system, dissolved organic carbon (DOC) is supplied by the continuous flow of wastewater and is aerobically decomposed by

a heterotrophic bacterial assemblage; it is then continuously discharged downstream. These stages constitute the fundamental components of actual ecosystems, such as constructed wetlands and lagoons. We assume two periodic fluctuations: the supply rate of DOC to the system and the maximum growth rate of bacteria (i.e., maximum biodegradation rate of DOC). We analyze the model using the basic theory of population ecology, a theory that has been applied to non-autonomous systems (Smith, 1981; Hale and Somolinos, 1983; Cushing, 1986).

2. Model

We consider a simple chemostat model (Smith and Waltman, 1995), which is applicable to a bacterial community with suspended growth. The dynamics of suspended (free-living) bacterial biomass in the water column (g m^{-3}), B, is given by:

$$V\frac{dB}{dt} = V(G(C, B) - mB) - qB, \tag{1}$$

where V is the volume (m^3) of the system, q is the continuous flow rate (m^3 day^{-1}). The first term on the right-hand side is the synthesis of biomass from DOC, the second represents the loss of biomass through maintenance processes and death, and the last term is the loss of biomass due to the outflow. We assume that the growth rate per unit volume (g m^{-3} day^{-1}), $G(C(t), B(t))$, depends on the DOC concentration in the water column (g m^{-3}), $C(t)$, and bacterial biomass. Further, we simply consider the bacterial communities to be a single population and the loss rate of biomass (day^{-1}), m, to be constant.

The dynamics of DOC concentration (g m^{-3}) is given by:

$$V\frac{dC}{dt} = qu(t) - qC - V\left(\frac{\alpha_C G(C, B)}{Y}\right) + Vr\alpha_C mB. \tag{2}$$

where $u(t)$ is the time-varying concentration of the DOC inflow (g m^{-3}), α_C is the carbon content per bacterial biomass, and Y represents the yield coefficient of biomass on DOC. The terms on the right-hand side are: (1) the inflow of allochthonous DOC (pollutant load) to the system, (2) the outflow of DOC from the system, (3) the loss rate of DOC due to catabolic and anabolic con-

sumption by bacteria, and (4) the reformation of DOC due to bacterial biomass decay. The loss and reformation of DOC occur in the water column V. We simply assume that biomass decay does not produce less labile compounds (but see Henze et al., 1996) and that a part r of it is recycled. We interpret metabolic loss for both biosynthetic processes $(1/Y - 1)\alpha_C G$, and maintenance processes $(1 - r)\alpha_C mB$, as biodegradation terms, but this does not mean everything is completely decomposed to CO_2. It could be converted to other forms of carbon, organic or inorganic, which may be less degradable, but are not considered here. If we assume a Monod's-type growth of bacteria, the growth rate, G, is given by:

$$G(C, B) = k(t)\frac{C}{C_S + C}B = g(C, t)B, \tag{3}$$

where C_S (g m^{-3}) is the half-saturation constant and $g(C, t)$ is the specific growth rate of bacteria. We assume that the effect of limiting factors other than DOC (e.g., nutrients, such as N and P, dissolved oxygen, and water temperature) is influenced, not by DOC and bacterial dynamics, but by external factors. We can assume that these factors are included in the term $k(t)$ (day^{-1}), the time-dependent maximum growth rate.

In this model, we assume that the two time-dependent functions ($u(t)$, the time-varying concentration of supplied DOC, and $k(t)$, the time-dependent maximum growth rate of bacteria) are periodic. Let $u(t)$ and $k(t)$ be functions with a period of τ (day), i.e.,

$$u(t + \tau) = u(t), \qquad k(t + \tau) = k(t).$$

The number of parameters appearing in the model (Eqs. (1) and (2)) is reduced when the following quantities are introduced:

$$\theta = \frac{t}{\tau}, \qquad x_1 = \frac{C}{C_S}, \qquad x_2 = \frac{\alpha_C B}{YC_S}, \qquad u' = \frac{u}{C_S},$$

$$\frac{q}{V} = \frac{1}{T_R}, \qquad m' = \left(m + \frac{q}{V}\right), \qquad Y' = \frac{m}{m'}rY.$$

Further, when symbol Y' and u' are replaced with Y and u, again Eqs. (1) and (2) are equivalent to:

$$\frac{dx_1}{d\theta} = \tau\frac{1}{T_R}u(\theta) - \tau\frac{1}{T_R}x_1$$
$$- \tau k(\theta)\frac{x_1}{1 + x_1}x_2 + \tau Ymx_2 \equiv f_1(\boldsymbol{x}, \boldsymbol{v}) \tag{4}$$

$$\frac{dx_2}{d\theta} = \tau k(\theta)\frac{x_1}{1 + x_1}x_2 - \tau m x_2$$
$$= \tau\{g(x_1, \theta) - m\}x_2 \equiv f_2(\boldsymbol{x}, \boldsymbol{v}), \quad (5)$$

where $\boldsymbol{x} = [x_1 \ x_2]^T$, $\boldsymbol{v} = [k \ u]^T$ and $g(x_1, \theta)$ is the time-dependent growth function of bacteria. Here, x_1, x_2, and $u(\theta)$ represent the DOC concentration, bacterial biomass, and supplied concentration of DOC, respectively, all of which are normalized by C_S (half saturation constant) and are dimensionless parameters. Further, note that $u(\theta)$ and $k(\theta)$ are rescaled to periodic functions with a period of 1 (we use the term 1-periodic function hereafter). Generally, the only condition that $u(\theta)$ and $k(\theta)$ must satisfy is that they are non-negative, respectively.

3. Results

We will discuss three types of dynamics: first, the time-autonomous system to provide the basis for subsequent analyses; second, the small fluctuations around the time-autonomous equilibrium in order to qualitatively investigate how temporal fluctuations influence system dynamics; and third, the dynamics under fluctuations with large amplitudes in order to quantitatively estimate the effect of temporal fluctuations on the biodegradation efficiency and to analyze the behavior that is absent when fluctuations are small.

3.1. The non-fluctuating system: two equilibria and their local stability

Here, we consider a time-autonomous system governed by Eqs. (4) and (5), where $u(\theta)$ and $k(\theta)$ are constant, respectively, i.e., $u(\theta) = u_0$, $k(\theta) = k_0$. Then, when $k_0 > m(1 + u_0)/u_0$, a system has two plausible equilibria. One is,

$$\boldsymbol{p}_0 = [u_0 \ 0]^T,$$

and the other is

$$\boldsymbol{p}_1 = [x_{1,0} \ x_{2,0}]^T = \left[\frac{m}{k_0 - m} \ \frac{u_0 - m/(k_0 - m)}{T_R m(1 - Y)}\right]^T,$$

whereas, only the former equilibrium $\boldsymbol{p}_0$ exists when $k_0 \le m(1 + u_0)/u_0$. At $\boldsymbol{p}_0$, the bacterial community is washed out, while it is maintained at $\boldsymbol{p}_1$, and the DOC

concentration $x_{1,0}$ is smaller than the supplied concentration u_0.

We analyzed the local stability of each equilibrium, calculating the eigenvalues of the Jacobian matrix evaluated at each equilibrium point (Smith and Waltman, 1995; and see Appendix A). When $k_0 > m(1 + u_0)/u_0$, $\boldsymbol{p}_0$ is unstable and $\boldsymbol{p}_1$ is asymptotically stable; whereas $\boldsymbol{p}_0$ is stable or asymptotically stable when the maximum growth rate is low ($k_0 \le m(1 + u_0)/u_0$). In the following sections, we consider cases where $k_0 > m(1 + u_0)/u_0$ holds. We will investigate whether the effects of temporal fluctuations are positive or negative, comparing temporal averages of DOC concentrations and bacterial biomass with the time-autonomous equilibrium $\boldsymbol{p}_1$.

3.2. The non-autonomous system under small fluctuations

We will analyze the dynamics under periodic fluctuations of k and u with small amplitudes ε, and, using perturbation techniques, will obtain a periodic solution analytically. Then, calculating the average values of x_1 (DOC concentration) and x_2 (bacterial biomass), we will show how these fluctuations interactively influence the dynamics of biodegradation systems.

We consider small oscillations around the average $\boldsymbol{v}_0$,

$$\boldsymbol{v}(\theta, \varepsilon) = \boldsymbol{v}_0 + \varepsilon\boldsymbol{v}_1(\theta) + \varepsilon^2\boldsymbol{v}_2(\theta) + \cdots$$
$$= \begin{bmatrix} k_0(1 + \varepsilon k_1(\theta) + \varepsilon^2 k_2(\theta) + \cdots) \\ u_0(1 + \varepsilon u_1(\theta) + \varepsilon^2 u_2(\theta) + \cdots) \end{bmatrix}, \quad (6)$$

where $\boldsymbol{v}_0 = [k_0 \ u_0]^T$, and $\boldsymbol{v}_i(\theta)$ is assumed to be a continuous 1-periodic function of θ with an average of zero. Under some natural conditions, a 1-periodic solution around $\boldsymbol{p}_1$, $\boldsymbol{x}(\theta, \varepsilon)$, is asymptotically stable when $k_0 > m(1 + u_0)/u_0$ holds, and it has the following form:

$$\boldsymbol{x}(\theta, \varepsilon) = \boldsymbol{x}_0 + \varepsilon\boldsymbol{x}_1(\theta) + \varepsilon^2\boldsymbol{x}_2(\theta) + \cdots = \begin{bmatrix} x_1(\theta, \varepsilon) \\ x_2(\theta, \varepsilon) \end{bmatrix}$$

$$= \begin{bmatrix} x_{1,0}(1 + \varepsilon x_{1,1}(\theta) + \varepsilon^2 x_{1,2}(\theta) + \cdots) \\ x_{2,0}(1 + \varepsilon x_{2,1}(\theta) + \varepsilon^2 x_{2,2}(\theta) + \cdots) \end{bmatrix}, \quad (7)$$

where each terms is a continuous function of θ (Appendix B). Substituting the expansions (6) and (7) into Eqs. (4) and (5) and equating coefficients of terms

with the same powers of ε on both sides of the resulting equations, we obtain equations satisfied by the coefficients $x_{i,j}(\theta)$ (Cushing, 1986). From the first two orders of these equations (Appendix B), we can calculate differences between the averages (av[$x_1(\theta, \varepsilon)$], av[$x_2(\theta, \varepsilon)$]) and equilibrium for the time-autonomous system ($x_{i,0}$) as follows:

$$\frac{\text{av}[x_i(\theta, \varepsilon)] - x_{i,0}}{x_{i,0}} = \varepsilon^2 \text{av}[x_{i,2}] + o(\varepsilon^2) \quad (i = 1, 2).$$

This means that the fluctuations $\boldsymbol{v}(\theta, \varepsilon)$ with the order of ε result in the deviation from equilibrium with the order of ε^2. This also means that the effects of fluctuations on the average DOC concentration and bacterial biomass can be determined only by calculating av[$x_{1,2}$] and av[$x_{2,2}$]. Then, we do not have to consider the actual order of the effects (ε^2), in order to qualitatively investigate the effects of temporal fluctuations. Therefore, we simply set $E_i = \text{av}[x_{i,2}]$ ($i = 1, 2$) as the index that represents the deviation from the time-autonomous equilibrium. In other words, we can consider that temporal fluctuations decrease the average DOC concentration (or the average bacterial biomass) below the time-autonomous equilibrium when $E_1 < 0$ ($E_2 < 0$), or increase this average when $E_1 > 0$ ($E_2 > 0$).

We obtain E_1 and E_2 as follows (Appendix B):

$$E_1 = \left(-\frac{1}{2} \frac{g_0''}{g_0'} x_{1,0} \right) \text{av}[x_{1,1}^2] - \text{av}[x_{1,1} k_1]$$
$$\quad - \frac{m}{g_0' x_{1,0}} \text{av}[x_{2,1} k_1] - \text{av}[x_{1,1} x_{2,1}] \tag{8a}$$

$$E_2 = -\frac{x_{1,0}}{m(1 - Y) T_R x_{2,0}} E_1, \tag{8b}$$

where g is the growth rate of bacteria given by Eq. (5) and

$$g_0' = \left. \frac{\partial g}{\partial x_1} \right|_{(k_0, x_{1,0})} > 0, \qquad g_0'' = \left. \frac{\partial^2 g}{\partial x_1^2} \right|_{(k_0, x_{1,0})}.$$

First, we note that the increase in the average bacterial biomass leads to the decrease in average DOC concentration, which is represented in Eq. (8b). In the following discussion, we describe a factor's effect as positive (or negative) on biodegradation when the factor enhances (or reduces) the bacterial average biomass, leading to a decrease (or increase) in the average DOC concentration.

Second, we give an interpretation of Eq. (8a) as follows. The first term on the right-hand side represents the effect of the temporal variability of DOC (av[$x_{1,1}^2$]) on the average growth rate. Only the form of the growth function g determines the sign of this effect. When bacteria exhibit a convex growth curve with respect to DOC, that is, a saturated growth rate (i.e., $g_0'' < 0$), the average DOC concentration increases. With a convex growth curve, the increase in growth rate with increased DOC ($g(x_{1,0} + \Delta x_1) - g(x_{1,0})$) is smaller than the decrease with decreased DOC ($g(x_{1,0}) - g(x_{1,0} - \Delta x_1)$). Therefore, fluctuations in DOC lead to a smaller (averaged) growth rate (i.e., $(1/2)\{g(x_{1,0} + \Delta x_1) + g(x_{1,0} - \Delta x_1)\} < g(x_{1,0})$), negatively affecting the rate of biodegradation. It follows that larger fluctuations lead to smaller bacterial biomass values and larger DOC concentrations. On the other hand, when bacteria exhibit a growth curve with a concave form (i.e., $g_0'' > 0$, an accelerated growth rate), the fluctuation of DOC has a positive effect on biodegradation. The remainder of the terms represent the effects of correlations between DOC concentration and the maximum bacterial growth rate (av[$x_{1,1} k_1$]), between bacterial biomass and its maximum growth rate (av[$x_{2,1} k_1$]), and between DOC and bacterial biomass (av[$x_{1,1} x_{2,1}$]), respectively. These terms represent the effects of correlations among fluctuations in determining the growth rate $k(\theta)\{x_1(\theta)/(1 + x_1(\theta))\}x_2(\theta)$. A positive correlation among fluctuations (a correlation between x_1 and k_1, between x_2 and k_1, or between x_1 and x_2) has a positive effect on bacterial growth and the degradation rate and results in a decreased DOC concentration.

Next, we examine how externally fluctuating factors, the maximum growth rate, and the supplied DOC concentration, determine the temporal variability of DOC and the correlations among fluctuations. We set the 1-periodic functions k_1 and u_1 explicitly as follows:

$$k_1(\theta) = \sum_{N=1}^{\infty} f_{k,N} \cos(2N\pi\theta + \varphi_{k,N}),$$

$$u_1(\theta) = \sum_{N=1}^{\infty} f_{u,N} \cos(2N\pi\theta + \varphi_{u,N}). \tag{9}$$

where the phases $\varphi_{u,N}$ and $\varphi_{k,N}$ are chosen so that $f_{k,N}$ and $f_{u,N}$ take positive values. Note that the order of $|k_1(\theta)|$ and that of $|u_1(\theta)|$ must be sufficiently small

that $\varepsilon|k_1(\theta)|$ and $\varepsilon|u_1(\theta)|$ have the order of ε, because we assumed the small fluctuations with the amplitude with the order of ε (see Eq. (6)).Using these expansions, we obtain a 1-periodic solution $(x_{1,1}, x_{2,1})$ representing the primary components of fluctuations in x_1 and x_2 (Appendix B). Substitution of this solution into Eq. (8a) yields:

$$E_1 = \sum_{N=1}^{\infty} C_{0,N} \{ C_{k,N}(f_{k,N})^2 + C_{u,N}(f_{u,N})^2$$
$$+ C_{ku,N}(f_{k,N} f_{u,N}) \cos(\varphi_{u,N} - \varphi_{k,N} - \Delta_N) \}$$
$$(10)$$

We obtain each coefficient $C_{X,N}$ ($N = 1, 2, 3, \ldots; X = 0, k, u, ku$) and phase Δ_N, which are independent of amplitudes ($f_{k,N}, f_{u,N}$), using the calculations in Appendix B.

The form of this equation provides insight into the effects of fluctuations k_1 and u_1. The first and second terms on the right-hand side are effects of temporal variability in the maximum growth rate and in the supplied DOC concentration, respectively. The third term represents an effect of interaction between these two fluctuations. Since $C_{0,N}$ is positive, $C_{k,N}$, $C_{u,N}$, and $C_{ku,N} \cos(\varphi_{u,N} - \varphi_{u,N} - \Delta_N)$ represent the sign of each effect. Although, the sign of $C_{k,N}$, and $C_{ku,N} \cos(\varphi_{u,N} - \varphi_{u,N} - \Delta_N)$ depend on several parameters, it is notable that $C_{u,N}$ is determined by the form of the growth curve ($C_{u,N} = (-1/2)(g''/g')(4N^2\pi^2\tau^2 u_0^2)(T_R^2 x_{1,0})^{-1}$).

This can be interpreted as follows. When the maximum growth rate does not fluctuate with a period of $1/N$ ($f_{k,N} = 0$), the bacterial community is not able to respond to fluctuations in the DOC supply rate with a period of $1/N$ ($f_{u,N} > 0$), and it is not able to effectively consume the DOC supplied (i.e., the effect of interaction is zero). When the fluctuations in supply rate are not moderated, the temporal variability of DOC ($\mathrm{av}[x_{1,1}^2]$) increases. As a result, the fluctuations in supply rate have negative effects on biodegradation when bacterial growth is saturated ($g_0'' < 0$), due to the mechanism mentioned above. Therefore, if $f_{k,N} = 0$ and $C_{u,N} > 0$, then $f_{u,N}$ should be zero to minimize E_1. Hereafter, we simply assume that $f_{k,N} = f_{u,N} = 0$ when $N > 1$ in Eq. (9). In other words, we only consider the case that two fluctuations (k_1 and u_1) are single sine curve with the same period. Note that we originally assumed more general form of fluctuations with multiple components of different periods (Eq. (9)). However, Eq. (10) means that there are no interactions between the components of different periods in these two fluctuations, because Eq. (10) is the linear summation of the effects of each component of different periods. Therefore, the above simplification is reasonable, when we consider the fluctuations with small amplitudes ε.

Next, we will show the effects of fluctuation characteristics, specifically, the effects of phase difference, amplitude, and period, on biodegradation using the growth function $g(x_1, \theta) = k(\theta)x_1/(1 + x_1)$ explicitly. We chose values for parameters based on literature values (Table 1). Note that we set the parameters to make the autonomous equilibrium p_1 asymptotically stable.

First, Fig. 1 represents the effect of phase differences between the maximum growth rate (k_1) and the supplied DOC concentration (u_1) on E_i, as computed by Eqs. (8a)–(10) for selected parameters (period is 1.0). Fig. 1a shows that the average DOC concentration is higher (i.e., $E_1 > 0$) or lower (i.e., $E_1 < 0$) than the equilibrium value of a non-fluctuating system ($x_{1,0}$) (solid line in Fig. 1a), depending upon the phase difference

Table 1
The parameter values for Eqs. (4) and (5)

Symbol	Definition	Value	Source
k_0	Maximum growth rate	0.6, 1.0, 6.0 day^{-1}	Billen et al. (1990), Morris and Lewis (1992), Henze et al. (1996)
Y	Yield	0.25	Henze et al. (1996), del Giorgio and Cole (1998)
m	Mortality	0.25 day^{-1}	Billen et al. (1990)
u_0	Supplied concentration of DOC normalized by C_S	0.5–10.0	Assumed
T_R	Residence time	10 day	Assumed

Note: The values of u_0 and T_R are assumptions; u_0 is a dimensionless value in Eqs. (4) and (5) and represents a ratio of u_0 to C_S (half saturation constant) in the original models (Eqs. (1) and (2)).
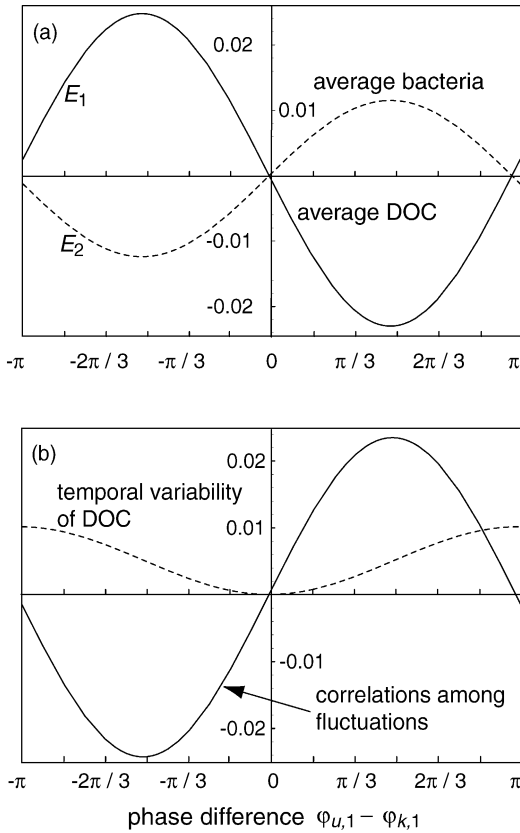
Fig. 1. The dependence of the average DOC concentration (E_1) and the average microbial biomass (E_2) on the phase difference ($\varphi_{u,1} - \varphi_{k,1}$). Panel (a) shows the average DOC concentration (solid line) and the average microbial biomass (dashed line). $E_i > 0$ represents larger values than the time-autonomous equilibrium ($x_{i,0}$). Parameters used are: $\tau = 1.0$, $f_{u,1} = 1.0$, $f_{k,1} = 1.0$, $u_0 = 1.0$, and $k_0 = 1.0$. Other parameters are described in Table 1. Panel (b) shows temporal variability in DOC concentration and correlations among fluctuations. We calculated $10 \times (-(1/2)(g_0''/g_0')x_{1,0})\mathrm{av}[x_{1,1}^2]$ and $\mathrm{av}[x_{1,1}k_1] + (m/g_0'x_{1,0})\mathrm{av}[x_{2,1}k_1] + \mathrm{av}[x_{1,1}x_{2,1}]$, respectively, depending on the phase difference. Parameters are the same as in (a).

($\varphi_{u,1} - \varphi_{k,1}$). As mentioned above, it also shows that the larger the average bacterial biomass (E_2), the lower the average DOC concentration (E_1).

It is notable that E_2 (i.e., the average bacterial biomass) is not largest when k_1 and u_1 are exactly in phase ($\varphi_{u,1} - \varphi_{k,1} = 0$). The average bacterial biomass is higher when fluctuations in the maximum growth rate and the DOC concentration are positively correlated. However, since fluctuations in x_1 are not exactly

in phase with u_1, that is, the peak DOC concentration occurs after the DOC supply rate peaks, this means that a positive correlation is attained with a phase difference. We make this clear by separating the effect of temporal variability of DOC and that of correlations among fluctuations in E_1 (the first term and the rest of the terms on the right-hand side of Eq. (8a)). Fig. 1b represents these two components and shows that the highest correlations are attained with differences in the phases (solid line).

Second, Eq. (10) defines how the amplitudes of fluctuations ($f_{k,1}$, and $f_{u,1}$) influence the average DOC concentration (E_1). In particular, the sign of the effect of u depends on the sum of two effects: (1) the temporal variability of u (the second term in Eq. (10)), which always negatively affects biodegradation and (2) the interaction with k (the third term in Eq. (10)), which depends on the phase difference. When the interaction between k and u has a negative effect on biodegradation (i.e., $C_{ku,1}\cos(\varphi_{u,1} - \varphi_{k,1} - \Delta_1) > 0$), the effect of u is always negative on biodegradation and the average DOC concentration increases monotonously with the amplitude $f_{u,1}$. On the contrary, when the effect of the interaction is positive (i.e., $C_{ku,1}\cos(\varphi_{u,1} - \varphi_{k,1} - \Delta_1) < 0$), the sign of the effect of u depends upon the amplitude $f_{u,1}$. When the relative amplitude of $f_{u,1}$ to $f_{k,1}$ is small, the resultant negative effect of the temporal variability of u, which leads to a larger temporal variability of DOC concentration ($\mathrm{av}[x_{1,1}^2]$), is smaller than the positive effect of the interaction ($\{C_{u,1}f_{u,1} + C_{ku,1}\cos(\varphi_{u,1} - \varphi_{k,1} - \Delta_1)f_{k,1}\}f_{u,1} < 0$), producing a net positive effect of u. Whereas, when the relative amplitude is sufficiently large, the sum of these two effects produces a negative effect of u ($\{C_{u,1}f_{u,1} + C_{ku,1}\cos(\varphi_{u,1} - \varphi_{k,1} - \Delta_1)f_{k,1}\}f_{u,1} > 0$). In this case, the effect of $f_{u,1}$ is not monotonous, and minimum E_1 (maximum E_2) is realized at an intermediate level of the amplitude. The minimum is realized at the $f_{u,1}$ value that satisfies the following equation:

$$
\begin{aligned}
\frac{\partial}{\partial f_{u,1}}&\{C_{u,1}(f_{u,1})^2 + C_{ku,1}(f_{k,1}f_{u,1}) \\
&\times \cos(\varphi_{u,1} - \varphi_{k,1} - \Delta_1)\} \\
&= 2C_{u,1}f_{u,1} + C_{ku,1} \\
&\quad \times \cos(\varphi_{u,1} - \varphi_{k,1} - \Delta_1)f_{k,1} = 0,
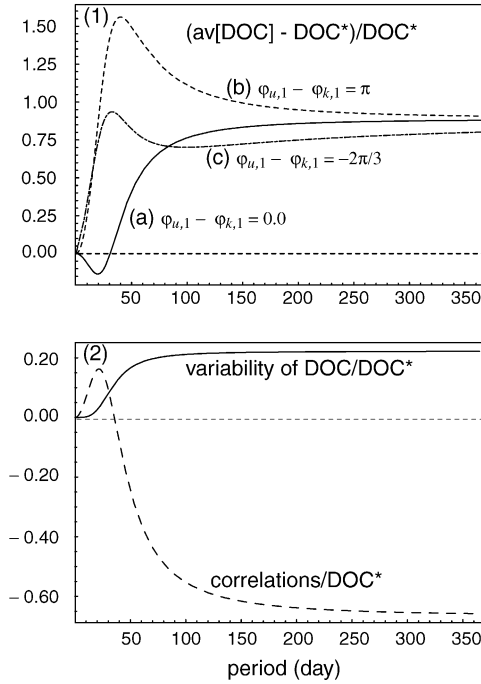\end{aligned}
$$

Fig. 2. The dependence of the average DOC concentration on the period of fluctuation. Panels show the average DOC concentration (E_1) depending on the period and the phase difference (Panel 1), temporal variability ($(-1/2)(g_0''/g_0')x_{1,0})\text{av}[x_{1,1}^2]$) and correlations among fluctuations $\text{av}[x_{1,1}k_1] + (m/g_0'x_{1,0})\text{av}[x_{2,1}k_1] + \text{av}[x_{1,1}x_{2,1}]$ (Panel 2). Parameters used are (1) $k_0 = 1.0$, $f_{u,1} = 1.0$, $f_{k,1} = 1.0$, $0.1 \le \tau \le 365$; (a) $\varphi_{u,1} - \varphi_{k,1} = 0.0$; (b) $\varphi_{u,1} - \varphi_{k,1} = \pi$; (c) $\varphi_{u,1} - \varphi_{k,1} = -2\pi/3$; (Panel 2) $\varphi_{u,1} - \varphi_{k,1} = 0.0$. Other parameters are described in Fig. 1, Panel 1. Here, DOC* denotes the equilibrium value of DOC in the time-autonomous system ($x_{1,0}$).

showing that this level depends on the amplitude of k ($f_{k,1}$).

Next, we show the dependence of E_1 on the period in fluctuations, τ (see Eq. (8) and Appendix B). Note that τ is the period of functions $u(t)$ and $k(t)$ in original model Eqs. (1) and (2), although they are rescaled to 1-periodic functions in Eqs. (4) and (5). The effect of the period depends on the phase difference (Fig. 2, Panel 1), but the relationship is not a simple one. When the period of fluctuation is long, the magnitude of the effect ($|E_1|$), whether positive or negative, tends to be much larger than the effect of fluctuations with a very short period (e.g., a 1-day period). Furthermore, the average DOC concentration tends to be higher than equilibrium for a time-autonomous system ($E_1 > 0$) when the period

of fluctuation is very long (e.g., a 365 day period). This is explained by the effects of the temporal variability of DOC and the correlations among fluctuations (Fig. 2, Panel 2). The DOC concentration ($x_1(\theta)$) and bacterial biomass ($x_2(\theta)$) tend to track the changes in u and k with increasing periods of fluctuations (Cushing, 1986) such that the temporal variability of DOC increases with the period. It follows that the magnitude of the effect increases with the period and that this negatively affects biodegradation. Moreover, correlations among fluctuations, i.e., the total effects of the three components, $\text{av}[x_{1,1}k_1]$, $\text{av}[x_{2,1}k_1]$, and $\text{av}[x_{1,1}x_{2,1}]$, tend to be negative (Fig. 2, Panel 2).

3.3. The system under large fluctuations

Finally, we consider the dynamics under periodic fluctuations of k and u with large amplitudes. Since, perturbation techniques are not applicable, we adopt a numerical method as well as an analytical method to obtain solutions and average values of x_1 and x_2. In the non-autonomous system governed by Eqs. (4) and (5), we consider the following large fluctuations:

$$\begin{pmatrix} k(\theta) \\ u(\theta) \end{pmatrix} = \begin{pmatrix} k_0(1 + f_k \cos(2\pi\theta)) \\ u_0(1 + f_u \cos(2\pi\theta + \varphi_u)) \end{pmatrix}, \qquad (11)$$

where we fix the timing of the peak k ($\varphi_k = 0$). The phase difference between k and u is φ_u, and the amplitudes must satisfy the inequality $0 < f_k, f_u < 1$ for positive $k(\theta)$ and $u(\theta)$.

In this section, we first analyze the behavior of a solution in the system of Eqs. (4) and (5) using Eq. (11) because the system exhibits behaviors different from the dynamics observed with small fluctuations. The solution can wildly deviate from periodic orbit around the time-autonomous equilibrium under certain conditions. Next, we calculate the effects of phase, amplitude, and period in order to compare the dynamics under conditions of large and small fluctuations and to quantitatively estimate the effects on "biodegradation efficiency", defined by $(u_0 - \text{av}[x_1])/u_0$. We also evaluate the magnitude of these effects, comparing the effects of temporal fluctuations and the influent load (average supplied concentration $u_0 \times$ flow rate q) on the effluent load (average outflow concentration $\text{av}[x_1] \times$ flow rate q).

3.4. Two distinct class solutions: maintenance or washout of the bacterial community

The system described by Eqs. (4) and (5) has two distinct classes of periodic solutions: (i) washout of the bacterial biomass, $x_2 = 0$; and (ii) maintenance of the bacterial community, $x_2 > 0$ for all $\theta \geq 0$. We can determine which solution is realized by analyzing the washout solution at the boundary,

$$B_2 = \{(x_1, x_2) \in \mathbf{R}^2 : x_1 \geq 0, \quad x_2 = 0\}.$$

Let the solution be $[\tilde{x}_1(\theta)\, 0]^{\mathrm{T}}$. Evaluating the local stability of this periodic solution $[\tilde{x}_1(\theta)\, 0]^{\mathrm{T}}$ (Appendix C) reveals that the washout solution is locally asymptotically stable if and only if

$$\mathrm{av}[g(\tilde{x}_1(\theta), \theta)] < m. \tag{12}$$

Eq. (12) means that the biomass of the bacterial community is not maintained when the average growth rate ($\mathrm{av}[g(\tilde{x}_1(\theta), \theta)]$) is smaller than the loss rate (m). Furthermore, it is shown that the washout solution is globally asymptotically stable if $\mathrm{av}[g(\tilde{x}_1(\theta), \theta)] < m$ and $1/T_{\mathrm{R}} < m(1 - Y)$ (Appendix C). The latter inequality tends to hold when bacterial loss is high or growth yield is low. On the other hand, the dynamic is proven to be permanent, i.e., bacteria are always maintained, when $\mathrm{av}[g(\tilde{x}_1(\theta), \theta)] > m$ (Appendix C). Therefore, the two classes of solutions are mutually exclusive.

The relationship between the two fluctuations k and u determines which solution is realized because Eqs. (11) and (12) are equivalent to:

$$1 - \frac{\sqrt{a_0^2 - a_1^2}}{a_0^2 - a_1^2} + \frac{f_k}{f_u} \frac{\sqrt{a_0^2 - a_1^2}(a_0 - \sqrt{a_0^2 - a_1^2})}{u_0(a_0^2 - a_1^2)\cos(\phi)}$$

$$\cos(\varphi_u - \phi) < \frac{m}{k_0}, \tag{13}$$

where $(\cos\phi, \sin\phi) = (4\pi^2 T_{\mathrm{R}}^2 + \tau^2)^{-1/2}[\tau, 2\pi T_{\mathrm{R}}]$ and $a_0 = u_0 + 1$, $a_1 = f_u \cos(\phi)u_0$.

This equation reveals that increasing the amplitude of fluctuations of the bacterial growth rate k (f_k) tends to wash out the bacterial community when the phase relationship is desynchronized (i.e., $\cos(\varphi_u - \phi)$ is negative), whereas it tends to maintain the bacterial community when the phase relationship is synchronized (i.e., $\cos(\varphi_u - \phi)$ is positive). Using Eq. (13) to investigate the stability of the washout solution, we can il-
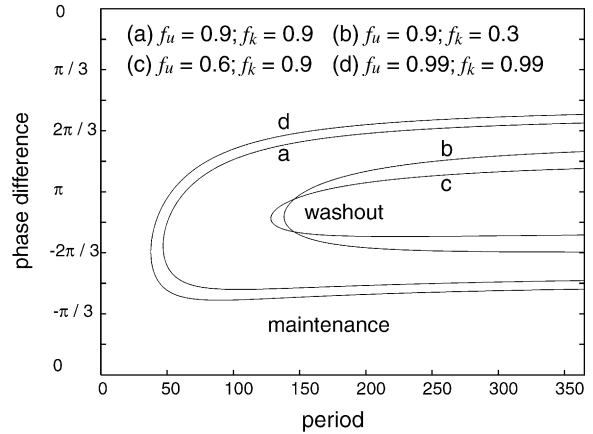

Fig. 3. The dependence of the realized stable state of the system on the period, the phase difference, and the amplitudes. This shows a combination of the period and the phase difference leading to a washout or maintenance of the bacterial community for different combinations of the amplitudes (f_k and f_u). The washout solution (or maintenance solution) is realized for values that lie to the inside (or outside) of a curve that corresponds to a particular combination of the amplitudes. Parameters used are: (a) $f_u = 0.9, f_k = 0.9$; (b) $f_u = 0.9$, $f_k = 0.3$; (c) $f_u = 0.6, f_k = 0.9$; and (d) $f_u = 0.99, f_k = 0.99$. Other parameters are described in Fig. 1.

lustrate which class of solution is realized, depending on periods, phase differences, and amplitudes of fluctuations, assuming a low growth rate of $k_0 = 0.6$ day^{-1} (Fig. 3). This analysis shows that bacterial biomass can be washed out depending on these parameters. This is the extreme outcome of the negative effect of fluctuations on bacteria, which is shown in the case of small-amplitude fluctuations.

3.5. Quantitative evaluations

To quantitatively evaluate the effects of temporal fluctuations on biodegradation, we used the Bulirsch–Stoer algorithm with adaptive step-size control for calculations (Press et al., 1988). Fig. 4 represents the effects of phase differences on the average DOC concentration (Fig. 4, Panel 1), the biodegradation efficiency (Fig. 4, Panel 1), the average bacterial biomass (Fig. 4, Panel 2), and the deviation from equilibrium for a time-autonomous system ($\mathrm{av}[x_1] - x_{1,0})/x_{1,0}$ (Fig. 4, Panels 3 and 4). These effects depend on the (average) maximum growth rate (k_0) and the period of fluctuations. When the period
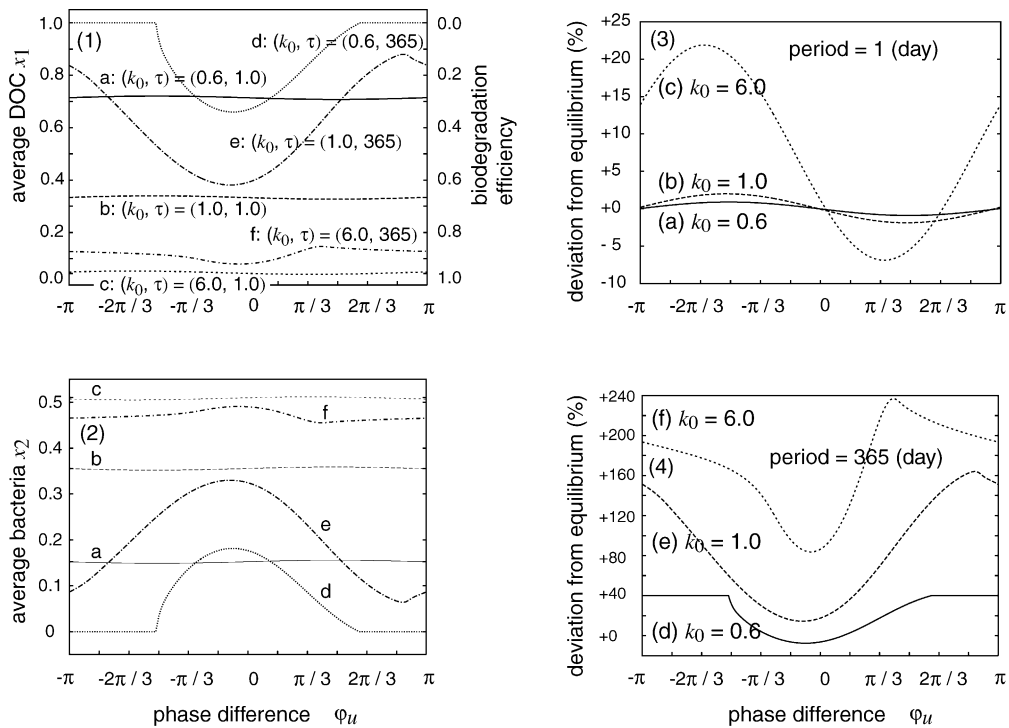
Fig. 4. The dependence of the averages of the DOC concentration and bacteria on the phase difference. Panel 1 shows the dependence of the average DOC $av[x_1]$ (the left axis) and biodegradation efficiency $(u_0 - av[x_1])/u_0$ (the right axis). Panel 2 shows the dependence of the average bacterial biomass $av[x_2]$. The deviation from the equilibrium DOC concentration is shown in Panel 3 (when $\tau = 1.0$ day) and Panel 4 (when $\tau = 365$ day). Parameters used in Panels 1–4 are (amplitudes): $f_u = f_k = 0.9$ in (a)–(f); (period): $\tau = 1.0$ in (a)–(c); 365 in (d)–(f); (average maximum growth rate): $k_0 = 0.6$ in (a) and (d); 1.0 in (b) and (e); 6.0 in (c) and (f).

is short (1 day), the average DOC concentration is quantitatively insensitive to phase differences (Fig. 4, Panel 1 and a–c), although, its dynamics are qualitatively the same as under small fluctuations (compare Fig. 4, Panel 3 and Fig. 1). On the other hand, when the period is long (365 days), the magnitude of the effect is not trivial (Fig. 4, Panel 1 and d–f), which is predicted by the effect of the period on the dynamics under conditions of small fluctuations. In particular, the deviation from values for a time-autonomous system is greater than 200% when the average maximum growth rate is large (6.0 day^{-1}) (Fig. 4, Panel 4 and f). As this deviation and negative effect on bacteria become much larger, bacterial biomass can converge to zero (washout), when the average maximum growth rate is small (0.6 day^{-1}) and the phase relationship is desynchronized (Fig. 4, Panel 2 and d), as mentioned above. We also show that the effects of am-

plitudes and period are qualitatively the same as in the case of small fluctuations (Fig. 5). The effect on biodegradation is primarily negative when the period is long, which is also predicted by the effect of the period on dynamics under conditions of small fluctuations.

Next, we quantitatively evaluate the effect of fluctuations, especially the effect of the phase difference, and compare that with the effect of influent DOC load. Fig. 6 shows the dependence of the average outflow DOC concentration ($av[x_1]$) on the average concentration of supplied DOC (u_0) and on the phase difference for a long period ($\tau = 365$ day). Note that $av[x_1]$ increases with increasing u_0, although the equilibrium DOC concentration $x_{1,0}$ is not influenced by u_0 in this model when u and k are not fluctuating. This is because a higher supplied DOC concentration (larger u_0) increases the temporal variation of DOC, and thus,
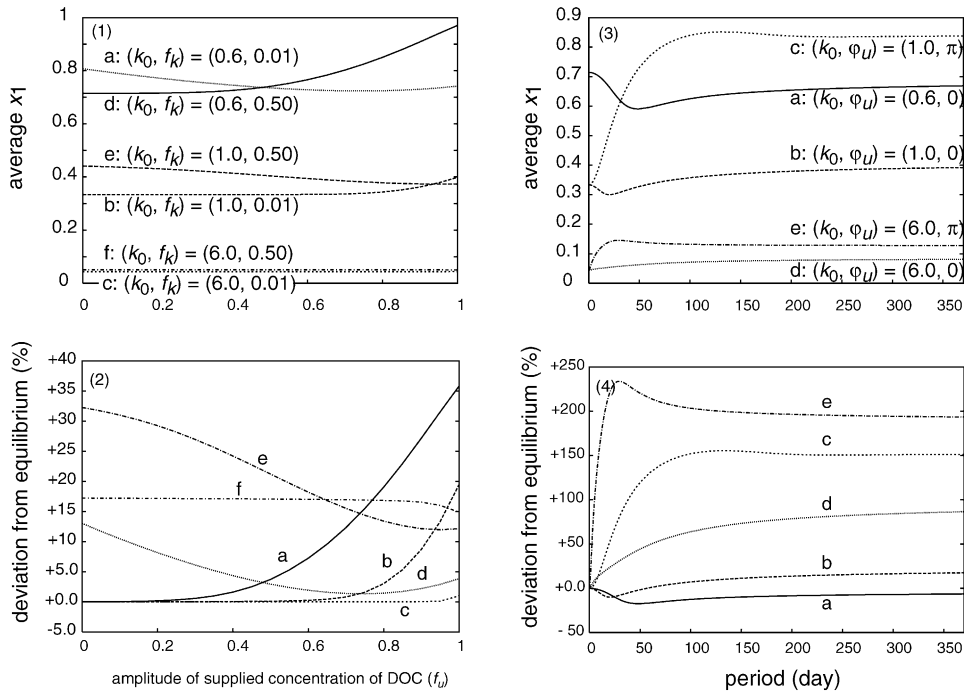
Fig. 5. The dependence of the average DOC concentration on the amplitudes and period of fluctuations. Panels 1 and 2 show the dependence of the average DOC concentration (Panel 1) and its deviation from the equilibrium (Panel 2) on the amplitude of u. Parameters used are: $\tau = 365$, $\varphi_u = 0.0$; (the amplitude of k): $f_k = 0.01$ in (a)–(c); 0.5 in (d)–(f); (maximum growth rate): $k_0 = 0.6$ in (a) and (d); 1.0 in (b) and (e); 6.0 in (c) and (f). Panels 3 and 4 show the dependence on the period of the average DOC concentration (Panel 3) and its deviation from the equilibrium (Panel 4). Parameters used are (amplitudes): $f_k = f_u = 0.9$ in (a)–(e); (phase difference): $\varphi_u = 0.0$ in (a), (b) and (d); $\varphi_u = \pi$ in (c) and (e); (maximum growth rate): $k_0 = 0.6$ in (a); 1.0 in (b) and (c); 6.0 in (d) and (e).

negatively affects biodegradation. The timing of the peak of u is different by one month between adjacent lines (i.e., the phase φ_u is different by $2\pi/12$), indicating that the average DOC concentration is very dependent on the phase relationship between the supply rate and the consumption rate. For example, compare the DOC concentration in the effluent load when the peak of u comes 3 months after that of k ($-3\tau/12$) with the DOC concentration of the effluent load when the peak of u comes 4 months after that k ($-4\tau/12$). The former is about 30% less than the latter. If the DOC concentration of the effluent has an approximately linear dependence on u_0 with a fixed phase difference, then the effect of changing the phase difference by only 1 month, from 4 to 3, is approximately equivalent to that of reducing DOC in the influent load by 30%, without changing the phase difference. This example highlights the large impact that temporal fluctuations have on biodegradation.

4. Discussion

This study investigates the effects of environmental variations on critical ecological processes and ecosystem functions. With a simple model of biodegradation, we demonstrate how two fluctuating factors (the supply rate of DOC and the maximum growth rate of bacteria) interactively influence an ecological process (the biodegradation of DOC) through modifying the community structure (the biomass of the bacterial community). Changes in the phase differences, the relative amplitudes, and the periods of these two fluctuating factors produce changes in the temporal variability of DOC, and in correlations among fluctuating factors. Whether changes in the temporal variability of DOC have positive or negative effects on biodegradation depends on the form of the bacterial growth curve with respect to DOC. Correlations among fluctuating factors may be positive or negative, depending upon several
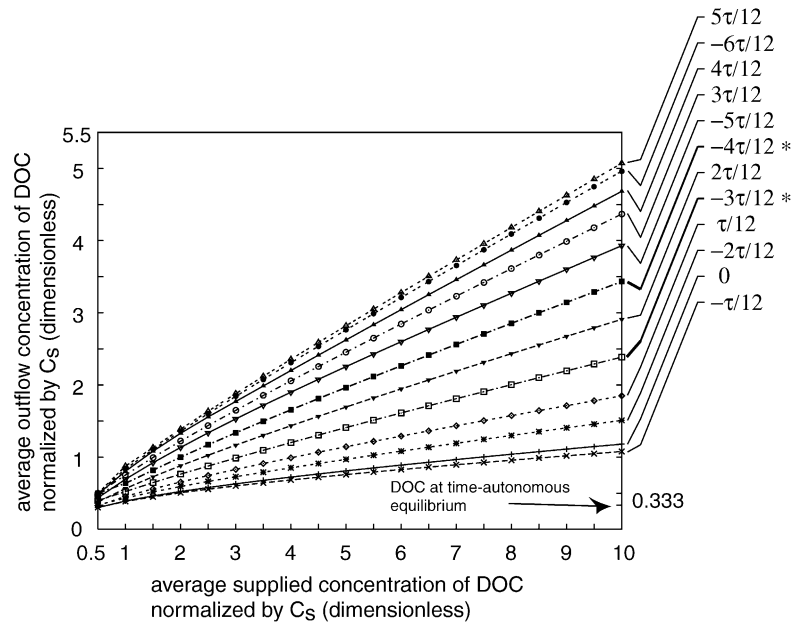
Fig. 6. The dependence of the outflow concentration of DOC on the supplied concentration of DOC and the phase difference. Each line shows the dependence on supplied concentration of DOC for different phase differences (φ_u). Calculations were made for every $2\pi/12$ with respect to φ_u, which is equivalent to making calculations for every $\tau/12$ in time scale t. We assume that $\tau = 365$ $k_0 = 1.0$, and $f_k = f_u = 0.9$. For example, compare the effluent load when the peak of u comes 3 months after that of k ($-3\tau/12$) with the effluent load when the peak of u comes 4 months after that of k ($-4\tau/12$). The former is about 30% smaller than the latter (when $u_0 = 10$, $2.3854/3.4322 \cong 0.695$).

factors, in particular, the period of, and phase difference between, fluctuations in the DOC supply rate and the maximum bacterial growth rate.

From a quantitative viewpoint, the magnitude of the effects of fluctuations depends on the average maximum bacterial growth rate (k_0) and the period of fluctuation (τ) (Fig. 4). When the period is short, the dependence of the biodegradation efficiency on the phase difference is very small, independent of maximum growth rate. When the period is long, the biodegradation efficiency is sensitive to the phase difference and the average maximum growth rate. A very slow bacterial growth rate leads to a washout of the bacterial community, which depends, in turn, on the phase difference; a rapid growth rate leads to high biodegradation efficiency, and this is independent of the phase difference. With intermediate growth rates, the dependence of the biodegradation efficiency on the phase difference is great (10–60%) and can generate a greater than two-fold difference in the average DOC concentration of the effluent (Fig. 4). An approximately equivalent change

in effluent DOC concentration is achieved (Fig. 6) by changing the average supply rate of DOC to a similar extent (10–60%). In other words, this model suggests that the effluent DOC load can be reduced effectively, even if the yearly averaged influent DOC load cannot be reduced. At the same time, it serves as a warning that DOC in the effluent load will increase with changing patterns of fluctuations, even if the influent DOC load is unchanged. In summary, this model theoretically predicts that the impacts of interactions between multiple fluctuations on the biodegradation depend on the traits of the fluctuations (e.g., the period), and on the traits of the biological community (e.g., growth rate).

Analytical investigations reveal the conditions under which the bacterial community is maintained or washed out (Fig. 3; Eq. (13); and Appendix C). The bacterial community cannot grow sufficiently during times of high substrate concentration and cannot survive a long term of low substrate supply, due to an asynchronous relationship between the growth rate and the DOC concentration; these conditions are represented

by long periods of fluctuation with large amplitudes. A washout of the bacterial community occurs when the loss rate of bacterial biomass (or maintenance energy) is constant, independent of growth conditions. Because bacterial catabolic and anabolic processes can change to optimize growth under sub-optimal conditions (see review: del Giorgio and Cole, 1998), a bacterial community would be less likely to be washed out. Even so, bacterial activities would be low and biodegradation would not proceed normally under conditions where the present model predicts a washout.

Our model and analyses provide useful results, but are simpler than an actual ecological treatment system (more generally, an aquatic ecosystem). First, in our model, temporal fluctuations are simply assumed to be periodic; non-periodic fluctuations are ignored. Furthermore, in most of the analyses, periodic fluctuations are also simplified to a single sine curve. It is necessary to consider the uncertainty of fluctuations and interactions among fluctuations with multi-periods in the context of the robust control of such a system. Second, we assumed bacterial growth kinetics simply as Monod's-type. However, non-monotonic growth, such as inhibition kinetics is known to lead to oscillatory dynamics even without external fluctuations (Ajbar and Ibrahim, 1997). Such autonomous oscillations are also observed in a physiologically structured-population model considering dynamics of the cell content (Pascual and Caswell, 1997). Interactions between fluctuations in internal dynamics and external factors would affect the biodegradation. Third, the model structure is too simple in that it neglects an important ecosystem process, that of autochthonous production by phytoplankton. Only allochthonous input and its consumption are included in our model. If temporal fluctuations in autochthonous production are also taken into account, there will be a greater temporal variability of DOC concentration, and the effects on the average DOC concentration may change drastically. Fluctuations of autochthonous production may buffer, or exacerbate, the asynchronous relationship between allochthonous input and its consumption. Competition between heterotrophic bacteria and phytoplankton for nutrients, such as nitrogen and phosphorus would also become important (Vadstein, 2000). These points may be considered in future work on theoretical and applied problems.

We have to discuss the differences between our model and other ecological models that consider tem-porally fluctuating factors. Kayombo et al. (2000) showed that multiple fluctuations (temperature, pH, and light intensity) were simultaneously influencing the temporal dynamics of dissolved oxygen. Furthermore, other studies pay attention to the differences in multiple temporal fluctuations and their influences on the ecosystem functions, such as water quality (Canu et al., 2003) and sea grass biomass (Elkalay et al., 2003). In Canu et al. (2003), the effects of physical forcing (wind and tide) on water quality are examined and compared them with the effect of reduction of nutrient load. Elkalay et al. (2003) showed that the relationship between the seasonal pattern of light intensity and that of sea grass growth was important for the production of sea grass. Such examinations are conceptually the same as our analysis, especially in Figs. 1, 4 and 6, showing the effects of phase difference between two fluctuations and comparing them with the equivalent effect of reduction of inflow load. However, in these studies, results are compared among only several scenarios of different patterns of external fluctuations. This might be because of the complexity of the models, preventing the detail analysis. Therefore, these studies only qualitatively suggest that the differences in fluctuations and the interactions among multiple fluctuations are important. However, they are not able to evaluate theoretically and quantitatively the effects of such differences on the ecosystem functions. In comparison to these models, out model is much simpler, and because of this simplicity, it has the following two advantages: (1) it was possible to analyze the response of the system to the continuous changes in the traits of fluctuations (phase, amplitudes, and periods) and (2) it was possible to reveal under what conditions the effects of external fluctuations become large, in other words, we detected some parameters determining the magnitude of the effects of fluctuations.

Our simple model is not intended to describe a specific ecosystem. Its quantitative estimations are rougher than various realistic models that can simulate the dynamics of material flows and biological communities (e.g., Wang and Mitsch, 2000; Koelmans et al., 2001; Rittmann et al., 2002). However, the numerical calculations have important implications, for example, that temporal fluctuations have primarily negative effects on the efficiency of biodegradation (Fig. 4, Panel 4; Fig. 5, Panels 3 and 4; and Fig. 6). Thus, evaluating the self-purification of ecosystems by using yearly

averaged values would be likely to yield overestimations. Although, it has been recognized that pulse-like events, such as temporally flashed loads, have negative effects on self-purification, we emphasize here that relatively slow, moderate, and predictable changes, like seasonal changes, also have considerable negative effects on biodegradation. This demonstrates the need to investigate the effects of periodic fluctuations on material cycling in order to more accurately evaluate and estimate the performance of ecological treatment systems. At the same time, it is important to develop methods of controlling temporal fluctuations in pollutant loads and biological community in order to reduce negative effects on the efficiency of biodegradation. As for biological community, recent theoretical and empirical studies suggest that community with higher species richness is less vulnerable to external fluctuations, leading to higher total biomass (Petchey et al., 2002). In this model, if we consider a single population as aggregate community, under the same fluctuations in external factors, the amplitude of fluctuating maximum growth rate f_k would be less in the community with higher richness. As for pollutant loads, controlling inflow rate (Smith and Waltman, 1995) or using settling ponds would be effective in order to relax the asynchronous phase relationship with bacterial activities. Changing the life style of people and modifying agricultural schedule (e.g., by changing the timing of fertilization), in order to control temporal fluctuations in pollutant concentration, are not the easiest ways but essentially necessary, if you take the long view.

Acknowledgements

Appendix A

In this appendix, we first calculate the partial derivatives, which are necessary for calculations in the Results section, and then analyze the local stability of equilibria in the time-autonomous system.

The partial derivatives of function $f = [f_1 f_2]^T$ are:

$$\frac{\partial f}{\partial x} = \begin{bmatrix} -\left(\dfrac{\tau}{T_R}\right) - \tau g_{x_1} x_2 & -\tau g + \tau Y m \\ \tau g_{x_1} x_2 & \tau g - \tau m \end{bmatrix}, \quad (A.1)$$

$$\frac{\partial f}{\partial v} = \begin{bmatrix} -\dfrac{\tau g x_2}{k} & \dfrac{\tau}{T_R} \\ \dfrac{\tau g x_2}{k} & 0 \end{bmatrix}, \quad (A.2)$$

$$\frac{\partial^2 f_1}{\partial y^2} = \begin{bmatrix} -\tau g_{x_1 x_1} x_2 & -\tau g_{x_1} & -\dfrac{\tau g_{x_1} x_2}{k} & 0 \\ -\tau g_{x_1} & 0 & -\dfrac{\tau g}{k} & 0 \\ -\dfrac{\tau g_{x_1} x_2}{k} & -\dfrac{\tau g}{k} & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix},$$

$$\frac{\partial^2 f_2}{\partial y^2} = \begin{bmatrix} \tau g_{x_1 x_1} x_2 & \tau g_{x_1} & \dfrac{\tau g_{x_1} x_2}{k} & 0 \\ \tau g_{x_1} & 0 & \dfrac{\tau g}{k} & 0 \\ \dfrac{\tau g_{x_1} x_2}{k} & \dfrac{\tau g}{k} & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}, \quad (A.3)$$

where $f = [f_1\ f_2]^T$, $y = [x_1\ x_2\ k\ u]^T$, $g(x_1) = kx_1/(1 + x_1)$.

Matrix (A.1) was evaluated at equilibria p_0 and p_1 to analyze the local stability of each. At $p_0 = [u_0\ 0]^T$, the matrix has the eigenvalues $\lambda_{0,1} = -\tau/T_R$, $\lambda_{0,2} = \tau(k_0 u_0/(1 + u_0) - m)$. When $k_0 \leq m(1 + u_0)/u_0$, p_0 is stable; otherwise p_0 is unstable. At

$$p_1 = [x_{1,0}\ x_{2,0}]^T = \left[\frac{m}{k_0 - m}\ \frac{u_0 - m/(k_0 - m)}{T_R m(1 - Y)} \right]^T,$$

the matrix has the following characteristic equation:

$$\lambda^2 + \left(\frac{\tau}{T_R} + \tau g_{x_{1,0}} x_{2,0} \right) \lambda + \tau^2 m(1 - Y) g_{x_{1,0}} x_{2,0} = 0$$

where

$$\left(\frac{\tau}{T_R} + \tau g_{x_{1,0}} x_{2,0} \right) > 0, \qquad \tau^2 m(1 - Y) g_{x_{1,0}} x_{2,0} > 0.$$

The roots of this equation are negative or have negative real parts; the equilibrium p_1 is asymptotically stable, if it exists.

Appendix B

First, we show the uniqueness of the periodic solution under small perturbations. Let $\boldsymbol{v}(\theta, \varepsilon)$ be continuous on $D = \{(\theta, \varepsilon) \in \boldsymbol{R}^2 : \theta \geq 0, 0 \leq \varepsilon \ll 1\}$. Then, given that a vector-valued function $\boldsymbol{f}(\theta, \boldsymbol{x}, \varepsilon) = [f_1(\theta, \boldsymbol{x}, \varepsilon) f_2(\theta, \boldsymbol{x}, \varepsilon)]^{\mathrm{T}}$ is continuous on $D \times \boldsymbol{R}_{+0}^2$ (Eqs. (4) and (5)) and differentiable with respect to $\boldsymbol{x}$ on $\boldsymbol{R}_{+0}^2$, and that $\partial \boldsymbol{f}/\partial \boldsymbol{x}$ is continuous on $D \times \boldsymbol{R}_{+0}^2$, it follows that $\boldsymbol{f}$ satisfies a Lipschitz condition in $\boldsymbol{x}$ on $\boldsymbol{R}_{+0}^2$. Under these conditions, theorems of ordinary differential equations (Coddington and Levinson, 1955; Theorems 1.1 and

1.2, Chapter 14) can be applied to the system of Eqs. (4) and (5) with Eq. (6), to yield the existence of a 1-periodic solution $\boldsymbol{x}(\theta,\varepsilon)$ and its uniqueness, which is continuous on D and satisfies $\boldsymbol{x}(\theta, 0) = \boldsymbol{p}_i$ $(i = 1, 2)$. Further, by Theorem 8.4 (Chapter 1), if $\boldsymbol{f}$ is assumed to be analytic in $(\boldsymbol{x}, \varepsilon)$, it follows that the solution around $\boldsymbol{p}_1$ has the form of Eq. (7) in which each term is a continuous function of θ.

Next, we solve the first two orders of these equations satisfied by the coefficients of Eq. (7) and obtained with (A.1)–(A.3). They have forms as follows:

$$\frac{\mathrm{d}}{\mathrm{d}\theta}\begin{bmatrix} x_{1,1} \\ x_{2,1} \end{bmatrix} = \tau \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & 0 \end{bmatrix}\begin{bmatrix} x_{1,1} \\ x_{2,1} \end{bmatrix}$$
$$+ \tau \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & 0 \end{bmatrix}\begin{bmatrix} k_1 \\ u_1 \end{bmatrix}, \quad (\text{B.1})$$

$$\frac{\mathrm{d}}{\mathrm{d}\theta}\begin{bmatrix} x_{1,2} \\ x_{2,2} \end{bmatrix}$$
$$= \tau \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & 0 \end{bmatrix}\begin{bmatrix} x_{1,2} \\ x_{2,2} \end{bmatrix} + \tau \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & 0 \end{bmatrix}\begin{bmatrix} k_2 \\ u_2 \end{bmatrix}$$
$$+ \tau \boldsymbol{h}(x_{1,1}, x_{2,1}, k_1), \quad (\text{B.2})$$

where

$$\tau \begin{bmatrix} a_{11} & a_{12} \\ a_{21} & 0 \end{bmatrix}$$
$$= \tau \begin{bmatrix} -\left(\dfrac{1}{T_{\mathrm{R}}} + g_0' x_{2,0}\right) & -m(1-Y)\left(\dfrac{x_{2,0}}{x_{1,0}}\right) \\ g_0' x_{1,0} & 0 \end{bmatrix} = \boldsymbol{A},$$

$$\tau \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & 0 \end{bmatrix} = \tau \begin{bmatrix} -m\left(\dfrac{x_{2,0}}{x_{1,0}}\right) & \dfrac{u_0}{T_{\mathrm{R}}x_{1,0}} \\ m & 0 \end{bmatrix} = \boldsymbol{B},$$

$$\boldsymbol{h}(x_{1,1}, x_{2,1}, k_1) = \begin{bmatrix} \left(-\dfrac{1}{2}\right) g_0'' x_{1,0} x_{2,0} x_{1,1}^2 - g_0' x_{2,0} x_{1,1} x_{2,1} - g_0' x_{2,0} x_{1,1} k_1 - m\left(\dfrac{x_{2,0}}{x_{1,0}}\right) x_{2,1} k_1 \\ \left(\dfrac{1}{2}\right) g_0'' x_{1,0}^2 x_{1,1}^2 + g_0' x_{1,0} x_{1,1} x_{2,1} + g_0' x_{1,0} x_{1,1} k_1 + m x_{2,1} k_1 \end{bmatrix},$$

and

$$g_0' = \left.\frac{\mathrm{d}g}{\mathrm{d}x_1}\right|_{x_1 = x_{1,0}} > 0, \qquad g_0'' = \left.\frac{\mathrm{d}^2 g}{\mathrm{d}x_1^2}\right|_{x_1 = x_{1,0}} < 0.$$

Then Eq. (B.2) yields,

$$\begin{bmatrix} \mathrm{av}[x_{1,2}] \\ \mathrm{av}[x_{2,2}] \end{bmatrix} = -\boldsymbol{A}^{-1}\mathrm{av}[\tau\boldsymbol{h}] = \frac{1}{a_{12}a_{21}}\begin{bmatrix} a_{12}\left\{\left(-\dfrac{1}{2}\right) g_0'' x_{1,0}^2 \overline{x_{1,1}^2} - g_0' x_{1,0}\overline{x_{1,1}x_{2,1}} - g_0' x_{1,0}\overline{x_{1,1}k_1} - m\overline{x_{2,1}k_1}\right\} \\ \left(\dfrac{1}{T_{\mathrm{R}}}\right)\left\{\left(-\dfrac{1}{2}\right) g_0'' x_{1,0}^2 \overline{x_{1,1}^2} - g_0' x_{1,0}\overline{x_{1,1}x_{2,1}} - g_0' x_{1,0}\overline{x_{1,1}k_1} - m\overline{x_{2,1}k_1}\right\} \end{bmatrix}.$$

By the Laplace transform, the linear system in Eq. (B.1) is equivalent to:

$$\boldsymbol{X}(s) = (s\boldsymbol{I} - \boldsymbol{A})^{-1}\boldsymbol{B}\boldsymbol{V}(s) + (s\boldsymbol{I} - \boldsymbol{A})^{-1}\boldsymbol{x}(0),$$

where $\boldsymbol{X}(s)$ and $\boldsymbol{V}(s)$ denote $\boldsymbol{X}(s) = \int_0^\infty \mathrm{e}^{-s\theta}\boldsymbol{x}_1(\theta)\,\mathrm{d}\theta$ and $\boldsymbol{V}(s) = \int_0^\infty \mathrm{e}^{-s\theta}\boldsymbol{v}_1(\theta)\,\mathrm{d}\theta$, respectively.

Here,

$$(s\boldsymbol{I} - \boldsymbol{A})^{-1}\boldsymbol{B}$$
$$= \frac{1}{s^2 - (\mathrm{tr}\boldsymbol{A})s + \det \boldsymbol{A}}$$
$$\times \begin{bmatrix} \tau b_{11}s + \tau^2 a_{12}b_{21} & \tau b_{12}s \\ \tau b_{21}s + \tau^2 a_{21}b_{11} - \tau^2 a_{11}b_{21} & \tau^2 a_{21}b_{12} \end{bmatrix}$$
$$= \begin{bmatrix} g_{11}(s) & g_{12}(s) \\ g_{21}(s) & g_{22}(s) \end{bmatrix}.$$

Using the expansions in Eq. (9), we can obtain a 1-periodic solution:

$$x_{1,1}(\theta) = \sum_{N=1}^{\infty} \left(\frac{1}{2}\right) \{f_{k,N} \exp(i\varphi_{k,N})g_{11}(i2N\pi)$$

$$+ f_{u,N} \exp(i\varphi_{u,N})g_{12}(i2N\pi)\} \exp(i2N\pi\theta)$$

$$+ \sum_{N=1}^{\infty} \left(\frac{1}{2}\right) \{f_{k,N} \exp(-i\varphi_{k,N})g_{11}(-i2N\pi)$$

$$+ f_{u,N} \exp(-i\varphi_{u,N})g_{12}(-i2N\pi)\}$$

$$\times \exp(-i2N\pi\theta),$$

$$x_{2,1}(\theta) = \sum_{N=1}^{\infty} \left(\frac{1}{2}\right) \{f_{k,N} \exp(i\varphi_{k,N})g_{21}(i2N\pi)$$

$$+ f_{u,N} \exp(i\varphi_{u,N})g_{22}(i2N\pi)\} \exp(i2N\pi\theta)$$

$$+ \sum_{N=1}^{\infty} \left(\frac{1}{2}\right) \{f_{k,N} \exp(-i\varphi_{k,N})g_{21}(-i2N\pi)$$

$$+ f_{u,N} \exp(-i\varphi_{u,N})g_{22}(-i2N\pi)\}$$

$$\times \exp(-i2N\pi\theta).$$

Using this solution, we obtain average values of $x_{1,1}x_{1,1}$, $x_{1,1}x_{2,1}$, $x_{1,1}k_1$, and $x_{2,1}k_1$ as follows, and then calculate E_i:

$$C_{N,0} = (\frac{1}{2})\{(\tau^2 a_{12}a_{21} + 4N^2\pi^2)^2 + \tau^2(2N\pi a_{11})^2\}^{-1}$$

$av[x_{1,1}x_{1,1}]$

$$= \sum_{N=1}^{\infty} C_{N,0}\{(f_{k,N})^2 \tau^4 (a_{12}b_{21})^2$$

$$+ (f_{k,N})^2 \tau^2 (2N\pi b_{11})^2 + (f_{u,N})^2 \tau^2 (2N\pi b_{12})^2$$

$$+ 2f_{k,N}f_{u,N}(2N\pi)^2 \tau^2 b_{11}b_{12} \cos(\varphi_{u,N} - \varphi_{k,N})$$

$$- 2f_{k,N}f_{u,N}2N\pi\tau^3 a_{12}b_{21}b_{12} \sin(\varphi_{u,N} - \varphi_{k,N})\}$$

$av[x_{1,1}x_{2,1}]$

$$= \sum_{N=1}^{\infty} C_{N,0}\{(f_{k,N})^2 \tau^4 a_{12}b_{21}(a_{21}b_{11} - a_{11}b_{21})$$

$$+ (f_{k,N})^2 \tau^2 (2N\pi)^2 b_{11}b_{21} + f_{k,N}f_{u,N}\tau^2 b_{12}b_{21}$$

$$\times (\tau^2 a_{12}a_{21} + 4N^2\pi^2) \cos(\varphi_{u,N} - \varphi_{k,N})$$

$$+ f_{k,N}f_{u,N}2N\pi\tau^3 a_{11}b_{12}b_{21} \sin(\varphi_{u,N} - \varphi_{k,N})\}$$

$av[k_1 x_{1,1}]$

$$= \sum_{N=1}^{\infty} C_{N,0}[-(f_{k,N})^2 \{\tau^2 a_{12}b_{21}$$

$$\times (\tau^2 a_{12}a_{21} + 4N^2\pi^2) + \tau^2 a_{11}b_{11}(2N\pi)^2\}$$

$$- f_{k,N}f_{u,N}(2N\pi)^2 \tau^2 b_{12}a_{11} \cos(\varphi_{u,N} - \varphi_{k,N})$$

$$+ f_{k,N}f_{u,N}2N\pi\tau b_{12}(\tau^2 a_{12}a_{21} + 4N^2\pi^2)$$

$$\times \sin(\varphi_{u,N} - \varphi_{k,N})]$$

$av[k_1 x_{2,1}]$

$$= \sum_{N=1}^{\infty} C_{N,0}[-(f_{k,N})^2 \{\tau^2 (a_{21}b_{11} - a_{11}b_{21})$$

$$\times (\tau^2 a_{12}a_{21} + 4N^2\pi^2) + \tau^2 a_{11}b_{21}(2N\pi)^2\}$$

$$- f_{k,N}f_{u,N}\tau^2 a_{21}b_{12}(\tau^2 a_{12}a_{21} + 4N^2\pi^2)$$

$$\times \cos(\varphi_{u,N} - \varphi_{k,N})$$

$$- f_{k,N}f_{u,N}2N\pi\tau^3 a_{11}a_{21}b_{12} \sin(\varphi_{u,N} - \varphi_{k,N})].$$

Notice that only $av[x_{1,1}x_{1,1}]$ includes the term with $f_{u,N}^2$ and the coefficient of $av[x_{1,1}x_{1,1}]$ in E_1;

$$-\left(\frac{1}{2a_{21}}\right)\tau g_0'' x_{1,0}^2$$

is positive, when g_0'' is negative.

Appendix C

We first analyze the local stability of the periodic solution of Eq. (4) with $x_2 = 0$. The linear equation $dx_1/d\theta = (\tau/T_R)u - (\tau/T_R)x_1$ has the following solution:

$$\tilde{x}_1 = u_0[1 + f_u\tau(4\pi^2 T_R^2 + \tau^2)^{-1}$$

$$\times \{\tau \cos(2\pi\theta + \varphi_u) + 2\pi T_R \sin(2\pi\theta + \varphi_u)\}]$$

$$= u_0[1 + f_u\tau(4\pi^2 T_R^2 + \tau^2)^{-1/2}$$

$$\times \cos(2\pi\theta + \varphi_u - \phi)], \tag{C.1}$$

where $\phi = \tan^{-1}(2\pi T_R/\tau)$.

The first variational equation with respect to this solution is:

$$\frac{\mathrm{d}z}{\mathrm{d}\theta} = \begin{bmatrix} -\dfrac{\tau}{T_R} & -\tau g(\tilde{x}_1, \theta) + \tau m Y \\ 0 & \tau g(\tilde{x}_1, \theta) - \tau m \end{bmatrix} z, \qquad \text{(C.2)}$$

where $z = (z_1, z_2)^T = (x_1 - \tilde{x}_1, x_2 - 0)^T$.

Then the multiplier of (C.2) can be computed (Smith, 1981):

$$\rho_1 = \exp\left(\frac{-\tau}{T_R}\right),$$

$$\rho_2 = \exp\left(\int_0^1 \tau\{g(\tilde{x}_1, s) - m\}\,\mathrm{d}s\right).$$

Thus, the periodic solution (C.1) is asymptotically stable if, and only if, $\int_0^1 \tau\{g(\tilde{x}_1, s) - m\}\,\mathrm{d}s < 0$, equivalent to Eq. (12), since $\tilde{x}_1$ is 1-periodic solution. Substituting explicitly the functions g and $\tilde{x}_1$ and calculating the integration yields Eq. (13). Furthermore, if $1/T_R < m(1 - Y)$ holds, we obtain the inequality $\mathrm{d}(x_1 + x_2)/\mathrm{d}t \leq T_R^{-1}(u(\theta) - (x_1 + x_2))$ from Eqs. (4) and (5), following that $x_1(\theta) + x_2(\theta) \leq \tilde{x}_1(\theta)$. This implies that $g(x_1(\theta), \theta) \leq g(\tilde{x}_1(\theta), \theta)$ because x_2 is non-negative (see the next paragraph), following that $\mathrm{d}(\ln x_2)/\mathrm{d}\theta \leq \tau(g(x_1, \theta) - m)$ from Eq. (5). Thus, when $\int_0^1 \tau\{g(\tilde{x}_1, s) - m\}\,\mathrm{d}s < 0$, $\ln x_2(\theta) - \ln x_2(0) \leq \int_0^\theta \tau\{g(\tilde{x}_1, s) - m\}\,\mathrm{d}s \to -\infty$ as $\theta \to \infty$ following that $x_2(\theta) \to 0$ exponentially as $\theta \to \infty$ (see the proof of Theorem 2.2 in Hale and Somolinos, 1983). Then, the washout solution is proved to be globally asymptotically stable (Smith, 1981).

Next, we obtain the sufficient condition of the permanence of the dynamics. The permanence for Eqs. (4) and (5) means that there exists an $\delta > 0$ such that

$$\delta < \liminf_{\theta \to \infty} x_i(\theta) \qquad \text{(C.3)}$$

for all i, whenever $x_i(0) > 0$ for all i, and there is an H such that

$$\limsup_{\theta \to \infty} x_i(\theta) \leq H \qquad \text{(C.4)}$$

for all i, whenever $x_0 \in \mathrm{int}R_+^2$.

We set the boundaries as follows: $B_1 = \{(x_1, x_2) \in R^2 : x_1 = 0, x_2 \geq 0\}$ and $B_2 = \{(x_1, x_2) \in R^2 : x_1 \geq 0, x_2 = 0\}$. On the boundary B_2, $\mathrm{d}x_2/\mathrm{d}\theta$ is zero and then

$$x_2(\theta) \geq 0 \quad \text{for all } \theta \qquad \text{(C.5)}$$

whenever $x_2(0) > 0$. On the boundary B_1, $\mathrm{d}x_1/\mathrm{d}\theta$ is always positive so that B_1 acts as a repellor, then (C.3) holds for $i = 1$. It also means that

$$x_1(\theta) > 0 \quad \text{for all } \theta \qquad \text{(C.6)}$$

whenever $x_1(0) > 0$.

We can prove that any solution starting in $R_{+0}{}^2$ is bounded as follows. From Eqs. (4) and (5), we obtain the inequality $\tau(T_R^{-1}u(\theta) - K_1 y) \leq \mathrm{d}y/\mathrm{d}\theta \leq \tau(T_R^{-1}u(\theta) - K_2 y)$, where $y = x_1 + x_2$, $\max(1/T_R, m(1 - Y)) = K_1$ and $\min(1/T_R, m(1 - Y)) = K_2$, which can be integrated to show that y is positive and bounded for all non-negative time (see Hale and Koçak, 1991, p. 124). Therefore, combined with Eqs. (C.5) and (C.6), Eq. (C.4) holds for $i = 1$ and 2.

Finally, we have to show for the permanence that Eq. (C.3) holds for $i = 2$ when $\mathrm{av}[g(\tilde{x}_1(\theta), \theta)] > m$. We can prove this using the average Lyapunov function (Hofbauer and Sigmund, 1998). We define the function P and Ψ as $P \equiv x_2^\beta$, $\Psi \equiv \dot{P}/P$, for any positive β. On the boundary B_2, it is easily proven that all solutions approach the periodic solution $\tilde{x}_1$ as $\theta \to +\infty$ (Hale and Koçak, 1991). From Eq. (5), we have $\Psi = \beta\tau\{g(x_1, \theta) - m\}$. Therefore, from Theorems 12.2.1 and 12.2.2 in Hofbauer and Sigmund (1998), Eq. (C.3) holds for $i = 2$ if $\int_0^1 \Psi(\tilde{x}_1)\,\mathrm{d}\theta > 0s$ is satisfied. This is equivalent to $\mathrm{av}[g(\tilde{x}_1(\theta), \theta)] > m$.

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