COMPLEX DYNAMICS IN A DISCRETE-TIME SIZE-STRUCTURED CHEMOSTAT MODEL WITH INHIBITORY KINETICS

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ABSTRACT. An inhibitory uptake function is incorporated into the discrete, size-structured nonlinear chemostat model developed by Arino et al. (Journal of Mathematical Biology, 45(2002)). Different from the model with a monotonically increasing uptake function, we show that the inhibitory kinetics can induce very complex dynamics including stable equilibria, cycles and chaos (via the period-doubling cascade). In particular, when the nutrient concentration in the input feed to the chemostat $S_0$ is larger than the upper break-even concentration value $\mu$, the model exhibits three types of bistability allowing a stable equilibrium to coexist with another stable equilibrium, or a stable cycle or a chaotic attractor.

1. Introduction. The chemostat is an important laboratory device that has been widely used for research in cell biology [8], ecology [4, 19] and evolutionary biology [11, 16, 20, 25, 26]. On the one hand, chemostat experiments can verify predictions made from mathematical modeling; On the other hand, chemostat experiments can provide some challenging problems in dynamical systems and stimulate the development of new mathematical theory. For instance, experiments by Hansen and Hubbell [14] successfully confirmed the theoretical results from mathematical analysis in [15]. Transient oscillations observed in experiments could be due to non-negligible micro-organism’s death and inhibitory kinetics as suggested by mathematical analysis in [24, 29].

Chemostat models mainly consist of differential equations including ordinary differential equations, delay differential equations and partial differential equations (see, for example, [7, 9, 10, 18, 22, 24, 27, 28, 29]). In discrete time steps, in order

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to model size structure, authors in [12] formulated a nonlinear matrix model for the evolution, considering a finite set of biomass classes. The discrete-time version of the LaSalle invariance principle is used in [2, 3] for the classical chemostat system to provide a more elegant analysis. In [23], Smith and Zhao extended the result to the \(n\)-species case by using Liapunov functions. The authors in [2] introduced inhomogeneous cell division size and analyzed nonzero globally stable equilibrium. However, these models are based on the assumption that the nutrient uptake and the cell growth function \(f\) is increasing and bounded satisfying \(f(0) = 0, f'(S) > 0\), and \(f''(S) < 0\), where \(S\) is the state variable representing the substrate concentration in the chemostat.

It has been pointed out by many scientists that certain substrates may be growth-limiting at low concentrations and growth-inhibiting at high concentrations [17]. This results in nonmonotone uptake functions. Some specific and general models of inhibitory kinetics have been discussed in [1, 5, 6, 7, 17]. For example, a specific functional form of inhibitory kinetics \(f(S) = \frac{m}{1 + bS + \frac{S}{c}}\) was used [5]. We note that the above mentioned studies considering functional form of inhibitory kinetics only considered in continue-time chemostat models.

In this paper, we aim to extend some results of [2] and [23] for one substrate and one population of microorganisms, to the case with inhibitory kinetics. We show that the inhibitory kinetics can induce very complex dynamics and three types of bistability can be observed. Most interestingly, for the two dimensional full model at the population level, each component is (numerically) shown to be chaotic, while the sum of the two components approaches a constant value.

We organize the rest of this paper as follows. For convenience, we present the model proposed in [2] and introduce our model assumptions in Section 2. We then analyze the limiting system in Section 3 and lift the obtained results to the full model in Section 4. Three types of bistability is numerically explored in Section 5. A brief summary and discussion is given in the last section.

2. The model and model assumptions.

The discrete, size-structured model of single specie on a limiting nutrient in the chemostat proposed in [2] is given by

\[
\begin{align*}
\dot{x}_t+1 &= (1 - E)A(S_t)x_t \\
\dot{S}_t+1 &= (1 - E)[S_t - f(S_t)U_t] + ES^0,
\end{align*}
\]

where \(t = 0, 1, \ldots\), the vector \(x_t \in \mathbb{R}^r_+, r = r_b + r_g + r_d > 0\), gives the distribution of biomass (in nutrient equivalent units) of the microbial population among \(r\) size classes at the \(t\)-th time step. There are \(r_b\) birth classes, \(r_d\) division classes, and \(r_g\) growth classes. \(S_t\) denotes the nutrient concentration at the \(t\)-th time step. \(S^0 > 0\) is the nutrient concentration in the input feed to the chemostat, \(E \in (0, 1)\) is the washout rate for the chemostat. The total biomass of the population at the \(t\)-th time step is given by \(U_t = x_t \cdot 1\), the scalar product of \(x_t\) and \(1 = (1, \ldots, 1) \in \mathbb{R}^r\). The nutrient uptake rate for the population is \(f(S)\). The transition matrix \(A(S_t)\) is given as

\[
A(S_t) = \begin{bmatrix}
A_{11} & A_{12} & A_{13} \\
A_{21} & A_{22} & A_{23} \\
A_{31} & A_{32} & A_{33}
\end{bmatrix},
\]
where $A_{12}$, $A_{23}$ and $A_{31}$ are zero matrices with sizes $r_b \times r_g$, $r_g \times r_d$ and $r_d \times r_b$, respectively, and

$$A_{11} = \begin{pmatrix} 1 - P_t & 0 & \cdots & 0 \\ MP_t & 1 - P_t & \cdots & 0 \\ 0 & \ddots & \ddots & \vdots \\ MP_t & 1 - P_t & \ddots & 0 \end{pmatrix}_{r_b \times r_b},$$

$$A_{22} = \begin{pmatrix} 1 - P_t & 0 & \cdots & 0 \\ MP_t(1 - D_1) & 1 - P_t & \cdots & 0 \\ 0 & \ddots & \ddots & \vdots \\ MP_t(1 - D_{rd-1}) & 1 - P_t & \cdots & 0 \end{pmatrix}_{r_g \times r_g},$$

$$A_{33} = \begin{pmatrix} 1 - P_t & 0 & \cdots & 0 \\ MP_t & 1 - P_t & \cdots & 0 \\ 0 & \ddots & \ddots & \vdots \\ MP_t & 1 - P_t & \ddots & 0 \end{pmatrix}_{r_d \times r_d},$$

$$A_{13} = \begin{pmatrix} MP_tD_1 \\ \vdots \\ MP_tD_{rd-1} \\ MP_t \end{pmatrix}_{r_b \times r_d},$$

$$A_{21} = \begin{pmatrix} 0 & \cdots & MP_t \\ \vdots & \ddots & \vdots \\ 0 & \cdots & 0 \\ \vdots & \vdots & \vdots \\ 0 & 0 & 0 \end{pmatrix}_{r_g \times r_b},$$

$$A_{32} = \begin{pmatrix} 0 & \cdots & MP_t \\ \vdots & \ddots & \vdots \\ 0 & \cdots & 0 \\ \vdots & \vdots & \vdots \\ 0 & 0 & 0 \end{pmatrix}_{r_d \times r_g},$$

with $P_t = f(S_t)/(M - 1)$, $M = 2^{r_b + r_g + r_d}$ and $D_i = D_i(S_t)$. We refer to [2] for further details.

With previous study carried out in [2, 12, 21, 23] in mind, in order for the model to make biological sense, throughout this paper, we always assume the following two assumptions.

- **(H1)**: The uptake function is in the form of $f(S) = \frac{aS}{1 + bS + cS^2}$, $S \in [0, +\infty)$, $a > 0, b \in \mathbb{R}_+, c > 0$. Moreover, the maximum uptake rate $m := \sup_{S \geq 0} f(S) = f(\sqrt{1/c}) = \frac{a}{b + 2c}$ satisfies $m < M - 1$;

- **(H2)**: The iteration period (or time step) $T$ satisfies

$$T \leq \min\left(\frac{M - 1}{m}, \frac{\ln 2}{(r_b + r_g + r_d)m}\right).$$

To study the dynamics of system (1), we may also need the following assumption.

- **(H3)**: If $aS^0 > 1$, it is required that $g(\xi) = (1 - E)(1 + f(\xi))(S^0 - \xi) \leq S^0$, where $\xi \in (0, S^0)$ is the unique positive solution of $h(v) = 0$ with $h(v)$ defined by

$$h(v) = c^2v^4 + 2bcv^3 + (b^2 + ab + 2c + acS^0)v^2 + 2(a + b)v + 1 - aS^0$$

for $v \in [0, S^0]$. 

3. Dynamics of the limiting system. Note that $1^T A(S_t) = [1 + (M - 1)P_1]1^T = (1 + f(S_t))1^T$. It then follows that the total biomass $U_t = 1^T x_t$ satisfies the difference equation
\[ U_{t+1} = 1^T x_{t+1} = 1^T A(S_t)x_t = (1 - E)(1 + f(S_t))U_t, \]
Let $Q_t = S_t + U_t$. By (3) and the second equation of (1), we find that $Q_t$ satisfies
\[ Q_{t+1} = (1 - E)Q_t + ES^0, \quad t \geq 0, \]
which results in
\[ Q_t = S^0 - (1 - E)^t(S^0 - Q_0), \quad t \geq 0. \]
and hence
\[ \lim_{t \to \infty} Q_t = S^0. \]
In view of $S_t = Q_t - U_t$ and $\lim Q_t = S^0$, we obtain the limiting system
\[ U_{t+1} = (1 - E)(1 + f(S^0 - U_t))U_t := G(U_t) \]
with the initial value $U_0 \in D$, where $D$ is defined as
\[ D := \{ U \in \mathbb{R}_+ : U \leq S^0 \}. \]

Our next result implies that $D$ is positively invariant for system (7), and hence (7) defines a discrete dynamical system on $D$.

**Lemma 3.1.** Assume $G(U)$ is defined in (7). Then the following statements hold.

(i) If $aS^0 \leq 1$, then $G(D) \subset D$ for $U \in [0, S^0]$ and $G'(U) > 0$;
(ii) If $aS^0 > 1$ and (H3) holds, then $G(D) \subset D$ for any $U \in [0, S^0]$. Furthermore, $G'(U) > 0$ for $U \in (0, S^0 - \xi)$ and $G'(U) < 0$ for $U \in (S^0 - \xi, S^0)$, where $\xi$ is defined in (H3).

**Proof.** It follows from (7) that $G(U) \geq 0$ for any $U \in [0, S^0]$. A direct calculation yields
\[ \frac{d}{dv}((1 + f(v))(S^0 - v)) = -\frac{h(v)}{(1 + bv + cv^2)^2}, \]
where $h(v)$ is defined in (2). By the chain rule, we have
\[ G'(U) = \frac{(1 - E)h(S^0 - U)}{(1 + b(S^0 - U) + c(S^0 - U)^2)^2}. \]

If $aS^0 \leq 1$, then clearly $h(S^0 - U) > 0$ for $U \in [0, S^0]$. Thus $G(U)$ is increasing in $U$ and $G(U) \leq G(S^0) = (1 - E)S^0 < S^0$ for $U \in [0, S^0]$. This proves $G(D) \subset D$.

Suppose $aS^0 > 1$. For any $v \in (0, S^0)$, we have $h'(v) > 0$ and $h(0) = 1 - aS^0 < 0$. Further, $h(S^0) = c^2(S^0)^4 + 2bc(S^0)^3 + (b^2 + 2c + ab + acS^0)(S^0)^2 + 2bS^0 + aS^0 + 1 > 0$. Thus $h(v) = 0$ admits a unique positive root $\xi \in (0, S^0)$ and $h(v) < 0$ for $v \in (0, \xi)$ and $h(v) > 0$ for $v \in (\xi, S^0)$. It follows from (9) that $G'(U) > 0$ for $U \in (0, S^0 - \xi)$ and $G'(U) < 0$ for $U \in (S^0 - \xi, S^0)$. This, together with (H3), implies $G(U) \leq G(S^0 - \xi) \leq S^0$.

In the case that $\frac{1}{1 + E} - 1 = \frac{E}{1 + E} < m = \sup_{S \geq 0} f(S)$, the equation $(1 - E)(1 + f(S)) = 1$ admits two positive solutions, which we denote by $\lambda$ and $\mu$ with $\lambda \leq \mu$. Note that these two solutions are referred to as the lower and upper break-even nutrient concentrations, respectively [27]. Further, we know that the function $f(S)$ is strictly increasing for $S \in [0, \lambda]$, and is strictly decreasing for $S \in [\mu, S^0]$ provided that $\mu \leq S^0$. 

Theorem 3.2. Suppose that $\frac{E}{1-E} < m$. Let $U_t$ be the solution of (7) with $0 < U_0 \in D$. For the case with $aS^0 \leq 1$ we have the following results.

(i) If $S^0 < \lambda$, then $\lim_{t \to \infty} U_t = 0$;
(ii) If $\lambda < S^0 < \mu$, then $\lim_{t \to \infty} U_t = S^0 - \lambda$;
(iii) If $\mu < S^0$, then $\lim_{t \to \infty} U_t = 0$ when $U_0 < S^0 - \mu$ and $\lim_{t \to \infty} U_t = S^0 - \lambda$ when $U_0 > S^0 - \mu$.

Proof. We first prove (i). Suppose $S^0 < \lambda$. We then have $(1-E)(1+f(S^0-U_t)) < 1$, and hence $U_{t+1} = (1-E)(1 + f(S^0 - U_t))U_t \leq U_t$. Note that for $U_0 \in D$ with $U_0 > 0$, we know $U_t \in D, t \geq 1$. Thus we obtain a sequence $\{U_t\}, t = 0, 1, \cdots$, which is decreasing and is bounded below from 0. Thus the sequence has a limit. In this case, the only fixed point of $G(U)$ is $U_0^* = 0$. Thus $\lim_{t \to \infty} U_t = 0$.

Next we consider the case with $\lambda < S^0 < \mu$. In this case $G(U)$ has two fixed points $U_0^* = 0$ and $U_1^* = S^0 - \lambda$. By Lemma 3.1, we know that $G(U)$ is increasing. If the initial value $U_0 \in (0, S^0 - \lambda)$, then $U_{t+1} = G(U_t) \leq G(S^0 - \lambda) = S^0 - \lambda$ and hence $U_t \in (0, S^0 - \lambda)$ for $t = 0, 1, \cdots$. This implies that $S^0 - U_t \in (\lambda, S^0)$ and $(1-E)(1+f(S^0 - U_t)) > 1$. Consequently, $U_{t+1} = G(U_t) = (1-E)(1+f(S^0 - U_t))U_t \geq U_t$. That is, the solution sequence $\{U_0, U_1, U_2, \cdots\}$ is increasing and bounded above by $S^0 - \lambda$. Thus $\lim_{t \to \infty} U_t = S^0 - \lambda$. If $U_0 \in (S^0 - \lambda, S^0)$, then $U_{t+1} = G(U_t) = (1-E)(1+f(S^0 - U_t))U_t \in (S^0 - \lambda, (1-E)S^0) \subset (S^0 - \lambda, S^0), t = 0, 1, \cdots$. Moreover, $S^0 - U_t \in (0, \lambda)$ and hence $0 < (1-E)(1+f(S^0 - U_t)) < 1$. This implies that the solution sequence $\{U_0, U_1, \cdots\}$ is decreasing and is bounded below by $S^0 - \lambda$. Again, $\lim_{t \to \infty} U_t = S^0 - \lambda$. This proves conclusion (ii).

If $\mu < S^0$, then the map $G(U)$ admits three fixed points $U_0^* = 0, U_1^* = S^0 - \lambda$ and $U_2^* = S^0 - \mu$. For the solution sequence $\{U_0, U_1, \cdots\}$ with $U_0 \in (0, S^0 - \mu)$. Similar to case (ii), we can show that $U_t \in (0, S^0 - \mu)$ and $U_{t+1} \leq U_t$. That is, the solution sequence is monotonically decreasing and is bounded below from 0. Thus $\lim_{t \to \infty} U_t = 0$. For $U_0 \in (S^0 - \mu, S^0 - \lambda)$, we have an increasing solution sequence with an upper bound $S^0 - \lambda$. It is then straightforward to verify that $\lim_{t \to \infty} U_t = S^0 - \lambda$.

If $U_0 \in (S^0 - \lambda, S^0)$, we can show that $U_t \in (S^0 - \lambda, S^0)$ and $\{U_t\}$ is decreasing. As a result, $\lim_{t \to \infty} U_t = S^0 - \lambda$. Therefore, $U_2^* = S^0 - \mu \in (0, S^0 - \lambda)$ is unstable, which separates the basins of attraction of two stable fixed points $U_0^*$ and $U_1^*$.

For the case $aS^0 > 1$, the monotonicity of the solution sequences cannot be guaranteed, the resulting dynamics of the map $U_{t+1} = G(U_t)$ can be very complex. In the following, we first present some stability result and then use bifurcation diagrams to illustrate the complex dynamics of (7).

Theorem 3.3. Assume that $\frac{E}{1-E} < m$, $aS^0 > 1$, and $G(S^0 - \xi) \leq S^0$, where $\xi$ is the unique positive solution of $h(v) = 0$ defined in (H3). Consider the limiting system (7) with $0 < U_0 \in D$, the following results hold:

(1) If $S^0 \leq \lambda$, then $\lim_{t \to \infty} U_t = 0$;

(2) If $\lambda < S^0 < \mu$, then $U_0^* = 0$ is unstable and $U_1^* = S^0 - \lambda$ is stable provided that

$$(1-E)(S^0 - \lambda)f'(\xi) < 2;$$

(10)

(3) If $S^0 > \mu$, then (3.a) $U_0^* = 0$ is stable and attracts solutions with $U_0 \in [0, S^0 - \mu]$; (3.b) $U_2^* = S^0 - \mu$ is unstable and (3.c) $U_1^* = S^0 - \lambda$ is stable if (10) holds.
Proof. The proof of conclusion (1) is identical to that of (i) in Theorem 3.2.

If \( \lambda < S^0 < \mu \), two fixed points are \( U_0^* = 0 \) and \( U_1^* = S^0 - \lambda \). It follows from (9) and \( S^0 \in (\lambda, \mu) \) that \( G'(0) = (1 - E)(1 + f(S^0)) > 1 \). Thus \( U_0^* = 0 \) is unstable. For the fixed point \( U_1^* = S^0 - \lambda \), its linear stability depends on \( G'(S^0 - \lambda) \). Note that \( G'(S^0 - \lambda) = 1 - (1 - E)(S^0 - \lambda)f'(\lambda) < 1 \) (since \( f'(\lambda) > 0 \)). We conclude that \( U_1^* = S^0 - \lambda \) is locally asymptotically stable if (10) holds.

If \( \mu < S^0 \), \( G(U) \) has three positive fixed points \( U_0^* = 0 \), \( U_1^* = S^0 - \lambda \) and \( U_2^* = S^0 - \mu \) satisfying \( 0 < S^0 - \mu < S^0 - \lambda \). In this case \( G'(0) = (1 - E)(1 + f(S^0)) \in (0, 1) \), thus \( U_0^* = 0 \) is stable. Moreover, we can show that \( [0, S^0 - \mu] \) is positively invariant and \( U_{t+1} = G(U_t) \leq U_t \) if \( U_t \in [0, S^0 - \mu] \). Therefore, if \( U_0 \in [0, S^0 - \mu] \), then the solution sequence is decreasing and \( \lim_{t \to \infty} U_t = U_0^* = 0 \). For the fixed point \( U_2^* = S^0 - \mu \), since \( \mu < S^0 \) and \( f'(\mu) < 0 \), we obtain

\[
G'(U_2^*) = 1 - (1 - E)(S^0 - \mu)f'(\mu) > 1.
\]

Therefore, \( U_2^* \) is unstable. The stability of \( U_1^* = S^0 - \lambda \) follows from the same linear stability analysis at in case (2).

Corollary 1. Under the assumptions of Theorem 3.3 with \( S^0 > \mu \), if \( G(S^0) < S^0 - \mu \), then there exists \( \eta \in (S^0 - \xi, S^0) \) such that \( G(\eta) = S^0 - \mu \). Thus \( U_0^* = 0 \) also attracts solutions with \( U_0 \in (\eta, S^0) \).

Proof. The existence of \( \eta \) follows from \( G(U) \) is decreasing for \( U \in (S^0 - \xi, S^0) \) and \( G(S^0) < S^0 - \mu \). If \( U_0 \in (\eta, S^0) \), then \( U_1 = G(U_0) \in (0, S^0 - \mu) \). As a consequence of conclusion (3.a), we have \( \lim_{t \to \infty} U_t = 0 \).

Remark 1. In Theorem 3.3, if (10) is not satisfied, i.e., \( G'(U_1^*) = G'(S^0 - \lambda) \leq -1 \), then \( U_1^* \) becomes unstable, a period-doubling cascade to chaos may occur. A representative bifurcation diagram illustrating the dynamics of (7) is presented in Figure 1 (for case (3.c)) (A similar bifurcation diagram can be obtained for case (2) as well).

![Bifurcation diagram for the discrete chemostat model](image)

**Figure 1.** Bifurcation diagram of the limiting system (7). Here \( f(s) = \frac{as}{1 + 0.1s} \), \( E = 0.1 \), \( S^0 = 100 \), \( U_0 = 70 \) with \( a \in [0.049, 0.059] \). Thus \( asS^0 > 1 \) and \( S^0 > \mu \). A cascade of period-doublings to chaos occurs as \( a \) increases.
4. **Dynamics of the full model.** In this section we consider the dynamics of the full size-structured model (1). To this end, we first lift the results for the limiting system (7) to the reduced system at the total population level, which is described by

\[
\begin{align*}
U_{t+1} &= (1 - E)(1 + f(S_t))U_t \\
S_{t+1} &= (1 - E)(S_t - f(S_t)U_t) + ES^0.
\end{align*}
\]  

(11)

The initial value \((U_0, S_0)\) associated with (11) is

\[(U(0), S(0)) \in \Omega := \{(U, S) \in \mathbb{R}^2_+: 0 \leq U + S \leq S^0\}.
\]

Denote by \(L\) the mapping determined by the right side of (11). They (11) can be rewritten as

\[(U_{t+1}, S_{t+1}) = L(U_t, S_t).
\]  

(12)

If \((U_t, S_t) \in \Omega\), then \(U_t \leq S^0 - S_t\) and \(S_{t+1} = (1 - E)(S_t - f(S_t)U_t) + ES^0 \geq p(S_t)\), where the function \(p(S)\) is given by

\[p(S) = (1 - E)(S - f(S)(S^0 - S)) + ES^0
\]

with \(p(0) = ES^0 < p(S^0) = S^0\). To ensure that \(L\) does define a discrete dynamical system on \(\Omega\), we need the following lemma.

**Lemma 4.1.** Consider \(p(S)\) defined in (13). If \(aS^0 \leq 1\), then \(p(S) > 0\); If \(aS^0 > 1\) then \(p(S) \geq 0\) provided that \((H3)\) is further satisfied.

**Proof.** Direct calculations yield

\[
p'(S) = (1 - E)[1 + f(S) + (S - S^0)f'(S)]
\]

\[= \frac{1 - E}{(1 + bS + cS^2)^2}h(S),
\]

where \(h(S)\) is defined in (2). In the case that \(aS^0 \leq 1\), it is clear that \(h(0) = 1 - aS^0 \geq 0\) and \(h(S) \geq h(0) \geq 0\). Thus \(p'(S) \geq 0\) and hence \(p(S) \geq p(0) = ES^0 > 0\). For the case \(aS^0 > 1\) we have \(h(0) = 1 - aS^0 < 0\) and there exists a unique value \(\xi \in (0, S^0)\) such that \(h(\xi) = 0\) and \(p(S) \geq p(\xi)\) for \(S \in [0, S^0)\). By \((H3)\), it follows from \(g(\xi) = (1 - E)(1 + f(\xi))(S^0 - \xi) \leq S^0\) that \(p(\xi) = S^0 - g(\xi) \geq 0\). This proves that \(p(S) \geq 0\) for \(S \in [0, S^0]\).

Let \((U_t, S_t)\) be the solution of (11) with \((U_0, S_0) \in \Omega\) and \(U_0 > 0\). Throughout this section, we always assume that \(\frac{E}{1 - E} < m\). Thus \(\lambda < \mu\) exist. Denote

\[
E_0 = (0, S^0), \ E_1 = (S^0 - \lambda, \lambda), \ E_2 = (S^0 - \mu, \mu).
\]

**Theorem 4.2.** Suppose that \(aS^0 \leq 1\). We have the following statements.

\[(I.1):\] If \(S^0 < \lambda\), then \(\lim_{t \to \infty} (U_t, S_t) = E_0;\)

\[(I.2):\] If \(\lambda < S^0 < \mu\), then \(E_0\) is unstable and \(\lim_{t \to \infty} (U_t, S_t) = E_1;\)

\[(I.3):\] If \(S^0 > \mu\), then both \(E_0\) and \(E_1\) are stable and \(E_2\) is unstable.

**Proof.** Since \(aS^0 \leq 1\), it follows from Lemmas 3.1 and 4.1 that \(L(U, S) \in \Omega\). That is, the set \(\Omega\) is positively invariant. Therefore system (11) defines a discrete dynamical system on \(\Omega\).

For the case with \(S^0 < \lambda\), it follows from \(S_t \leq S^0 < \lambda\) and \(f(S)\) is increasing for \(S \in [0, \lambda]\) that \((1 - E)(1 + f(S_t)) < (1 - E)(1 + f(\lambda)) = 1\). This leads to \(U_{t+1} < U_t\).
On the other hand, $S_t \leq S^0 < \lambda$ implies that $(1 - E) f(S_t) < E$. Consequently
\[
S_{t+1} = (1 - E)(S_t - f(S_t) U_t) + ES^0 \\
= S_t + E(S^0 - S_t) - (1 - E)f(S_t) U_t \\
\geq S_t + E(S^0 - S_t) - EU_t \\
= S_t + E(S^0 - S_t - U_t) \geq S_t.
\]

The monotonicity and boundedness of $\{U_t\}$ and $\{S_t\}$ show that $\lim_{t \to \infty} U_t = U^* \leq S^0$ and $\lim_{t \to \infty} S_t = S^* \leq S^0$ exist. From the first equation of (11), we have $U^* = (1 - E)(1 + f(S^*)) U^*$. This, together with $(1 - E)(1 + f(S^*)) < 1$, immediately shows that $\lim_{t \to \infty} U_t = U^* = 0$. Taking the limit on both sides of the second equation of (11) yields $\lim_{t \to \infty} S_t = S^* = S^0$.

Now we consider the case $\lambda < S^0 < \mu$. In this case, $(1 - E)(1 + f(S^0)) > 1$ and system (11) admits two feasible fixed points, $E_0$ and $E_1$. Standard linear stability analysis shows that the two eigenvalues associated with the Jacobian matrix of $L$ at $E_0$ are $1 - E \in (0, 1)$ and $(1 - E)(1 + f(S^0)) > 1$. This shows that $E_0$ is unstable and is indeed a saddle point with the stable manifold given by $\{(0, S) : S \in [0, S^0]\}$. As in [21], the two eigenvalues of the Jacobian matrix of $L$ at $E_1$ are $1 - E$ and $1 - (1 - E)(S^0 - \lambda)f'(\lambda)$. Since $\frac{E}{1 - E} < m$, $0 < \lambda < \sqrt{1/c}$ and $f''(S) < 0$ for $S \in (0, \sqrt{1/c})$, $(S^0 - \lambda)f'(\lambda) < S^0f'(0) = aS^0 \leq 1$. Thus both eigenvalues are in $(0, 1)$ and hence $E_1$ is locally asymptotically stable.

Since $U_0 > 0$, it follows from (11) that $U_t > 0$, $\forall t > 0$. Clearly the initial condition $(U_0, S_0)$ is not in the stable manifold of $E_0$. As in the proof of [21, Theorem 2.4], for the orbit $\{(U_t, S_t)\}_{t \geq 0}$, let $\Lambda$ be its omega limit set. Then $\Lambda$ is a nonempty, compact, invariant subset in the line segment $U + S = S^0$ in $\Omega$. From the dynamics of $L$ restricted to this line segment and note that $E_0 \notin \Lambda$, we see that $\Lambda$ contains $E_1$ and hence $\lim_{t \to \infty} (U_t, S_t) = E_1$.

Suppose that $S^0 > \mu$. Then three fixed points, $E_0$, $E_1$ and $E_2$ of system (11) are all feasible. Note that $(1 - E)(1 + f(S^0)) < 1$, $aS^0 \leq 1$, $f'(\lambda) > 0$ and $f'(\mu) < 0$. For the Jacobian matrix of (11) at $E_0$, both eigenvalues $1 - E$ and $(1 - E)(1 + f(S^0))$ belong to $(0, 1)$ and hence $E_0$ is locally asymptotically stable. The local stability of $E_1$ can be similarly proved as for the case $\lambda < S^0 < \mu$. At the fixed point, $E_2$, one eigenvalue of its Jacobian matrix is $1 - (1 - E)(S^0 - \mu)f'(\mu) > 1$, the other eigenvalue is $1 - E$. Thus $E_2$ is unstable.

\begin{proof}
It follows from Lemma 4.1 and (5) that $L(U, S) \in \Omega$ and thus system (11) defines a discrete dynamical system on $\Omega$. Proof of (II.1) is the same as the proof of (I.1) in Theorem 4.2. (II.2) follows from linear stability analysis. In this case, for the fixed point, the Jacobian matrix has two eigenvalues, one is $1 - E \in (0, 1)$ and the other is $1 - (1 - E)(S^0 - \lambda)f'(\lambda) < 1$. Thus $E_1$ is stable provided (10) holds and is unstable if (10) is not satisfied. (III.c) follows from the same argument as in the proof of (I.3) in Theorem 4.2.
\end{proof}
Remark 2. Denote by $\tilde{U}_t$ the solution of (7) with $\tilde{U}_0 \in D$ and $\tilde{U}_0 = U_0 > 0$. Even though the stability condition for the fixed point $U^*_1 = S^0 - \lambda$ of the limiting system (7) is the same as that for the fixed point $E_1 = (S^0 - \lambda, \lambda)$ of the full model at the population level i.e., system (11) (as can be seen from Theorems 3.3 and 4.3), we should point out that the solution $\tilde{U}_t$ of the limiting system (7) approaches zero does not necessarily imply $U_t$ of (11) tends to zero. In other words, $\lim_{t \to \infty} \tilde{U}_t = 0$ does not imply $\lim_{t \to \infty} (U_t, S_t) \to (0, S^0)$. To illustrate this, we take $a = 0.05$, $b = 0.1$, $c = 0.01$, $S^0 = 100$, $E = 0.1$. Then $\lambda \approx 3.1386$, $\mu \approx 31.8614$. Based on Theorem 3.3, if $U_0 < S^0 - \mu$, then the solution $\tilde{U}_t$ of (7) satisfies $\lim_{t \to \infty} \tilde{U}_t = 0$. If we take $U_0 = 60 < S^0 - \mu \approx 68.1386$, as seen from the left panel of Figure 2, $\tilde{U}_t$ does approach 0, while for system (11) with $(U_0, S_0) = (60, 6)$, the total biomass $U_t$ satisfies $\lim_{t \to \infty} U_t = S^0 - \lambda \approx 96.8614$ (See the right panel of Figure 2).

To describe the dynamics of the full model (1), we first define the set $\Gamma$ as

$$
\Gamma = \{(x, S) \in \mathbb{R}_r^{r+1} : x \cdot 1 + S \leq S^0\}.
$$

It follows from the positive invariance of $\Omega$ for (11) that the set $\Gamma$ is positively invariant with respect to (1). As in [2, 21, 23], by using the weak ergodic theorem of Golubitsky et al. [13, Corollary 3.2], we can obtain the following result illustrating the biomass has a stable uniform size distribution.

**Theorem 4.4.** Consider (1). For any $(x_0, S_0) \in \Gamma$ with $x_0 \cdot 1 > 0$, if the solution $(U_t, S_t)$ of (11) satisfies $\lim_{t \to \infty} (U_t, S_t) = (S^0 - \lambda, \lambda)$, then

$$
\lim_{t \to \infty} x_t = \frac{S^0 - \lambda}{r} 1.
$$
5. Bistability: Numerical exploration. Note that when the nutrient concentration in the input feed to the chemostat $S^0$ is larger than the upper break-even concentration value $\mu$, for system (11), the washout fixed point $E_0$ is stable, while dynamics of the fixed point $E_1$ is complex. In this section, we numerically explore possible dynamics. In particular, we demonstrate that system (11) exhibits three types of bistability, namely, type-I: the stable fixed point $E_0$ coexists another stable fixed point $E_1$; type-II: the stable fixed point $E_0$ coexists with a stable cycle; and type-III: the stable equilibrium $E_0$ coexists with a chaotic attractor.

To numerically demonstrate three types of bistability, we fix parameter values $b = 0.1$, $c = 0.01$, $S^0 = 100$, $E = 0.1$ and vary the value of $a$. First, we take $a = 0.05$. Calculations yield $\lambda \approx 3.1386$, $\mu \approx 31.8614$. Assumptions of Theorem 4.3 are satisfied and $(1 - E)(S^0 - \lambda)f'(\lambda) \approx 1.9698 < 2$. Thus both $E_0$ and $E_1$ are stable. Bistability of type-I occurs, and is demonstrated in Figure 3.

Now we take $a = 0.054$, then $\lambda \approx 2.7927$, $\mu \approx 35.8073$. All assumptions of Theorem 4.3 are satisfied and $(1 - E)(S^0 - \lambda)f'(\lambda) \approx 2.3645 > 2$. Thus $E_0$ is stable and $E_1$ is unstable, numerical simulations show that a cycle appears with $U_t$ oscillating about $S^0 - \lambda$. The model outcome is initial condition dependent, bistability of type-II emerges. A representative figure is presented in Figure 4.

**Figure 3.** Numerical solutions of system (11) with $f(s) = \frac{0.05s}{1+0.1s+0.017s^2}$, $E = 0.1$, $S^0 = 100$. Left: $(U_t, S_t) \to E_0 = (0, S^0)$ as $t \to \infty$, initial condition $(U_0, S_0) = (10, 6)$ was used; Right: $(U_t, S_t) \to E_1 = (S^0 - \lambda, \lambda)$ as $t \to \infty$, initial condition was $(U_0, S_0) = (80, 6)$.

**Figure 4.** Numerical solutions of system (11) with $f(s) = \frac{0.054s}{1+0.1s+0.017s^2}$, $E = 0.1$, $S^0 = 100$. Left: $(U_t, S_t) \to (0, S^0)$ as $t \to \infty$, initial condition $(U_0, S_0) = (10, 6)$ was used; Right: $(U_t, S_t)$ approaches a stable $2 - cycle$, initial condition was $(U_0, S_0) = (80, 6)$. 
Let $a = 0.059$. Then $\lambda \approx 2.4607$, $\mu \approx 40.6393$. All assumptions of Theorem 4.3 are satisfied and $(1 - E)(S^0 - \lambda)f'(\lambda) = 2.85 > 2$. Thus $E_0$ is stable and $E_1$ is unstable. Numerical solutions with two sets of initial conditions, $(U_0, S_0) = (10, 6)$ and $(U_0, S_0) = (80, 6)$, are plotted in Figure 5. As shown in Figure 5, bistability of type-III is observed. It is interesting to note that when $(U_0, S_0) = (80, 6)$, though $S_t + U_t \to S^0$, componentwise, both $S_t$ and $U_t$ behave chaotically.

**Figure 5.** Numerical solutions of system (11) with $f(s) = 0.059s^0 + 0.1s + 0.01s^2$, $E = 0.1$, $S^0 = 100$. Left: $(U_t, S_t) \to (0, S^0)$ as $t \to \infty$, initial condition $(U_0, S_0) = (10, 6)$ was used; Right: $(U_t, S_t)$ approaches a chaotic attractor, initial condition was $(U_0, S_0) = (80, 6)$.

6. **Summary.** In this paper, we have incorporated a specific inhibitory uptake function into the discrete, size-structured chemostat model developed in [2]. Our results demonstrate that the inhibitory kinetics can induce very complex dynamics. Even for the limiting system (7), the attractor can either be a fixed point, a cycle or a chaotic attractor (See Figure 1). For the full model at the population level, system (11) with $aS^0 > 1$, if the nutrient concentration in the input feed to the chemostat $S^0$ is larger than the upper break-even concentration value $\mu$, we have shown that the model outcome is initial-condition dependent, and the model exhibits three types of bistability (See Figures 3-5). This phenomenon of bistability can never occur when the uptake function is monotonically increasing [21].

It is interesting to note that though the sum of the total biomass and the nutrient approaches a constant value, i.e., $U_t + S_t \to S^0$ as $t \to \infty$, componentwise, the total biomass $U_t$ and the nutrient concentration $S_t$ can both be chaotic (See Figure 5). Moreover, as pointed out in Remark 2, when the uptake function is inhibitory, the solution behavior of the limiting system and that of the full model may not be necessarily equivalent. More precisely, for the total biomass (the $U$ component) alone, the basins of attraction may be different, the initial nutrient concentration does play a role in determining the model outcome.

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