4

A Discrete-Time Chemostat Model

The chemostat is an important laboratory apparatus used for the continuous culture of microorganisms. In ecology it is often viewed as a model of a simple lake system, of the wastewater treatment process, or of biological waste decomposition. Mathematical models of microbial growth and competition for a limiting substrate in a chemostat have played a central role in population biology. See [334] for a treatment of chemostat models. However, the classical model ignores the size structure of the population and the observation that many microbes roughly double in size before dividing. Size-structured chemostat models formulated by Metz and Diekmann [248] and by Cushing [76] lead to hyperbolic partial differential equations with nonlocal boundary conditions. A conceptually simpler approach to modeling size structure was taken by Gage, Williams and Horton [127], who formulated what is now referred to as a nonlinear matrix model for the evolution, in discrete-time steps, of a finite set of biomass classes. Smith [327] modified this model and showed that competitive exclusion holds for two competing microbial populations. The purpose of the present chapter is to give a thorough mathematical analysis of this model of any number of competing populations.

In Section 4.1 we introduce the model under some appropriate assumptions, and derive a conservation principle for the total nutrient. In Section 4.2 we show that the model leads to a lower-dimensional system of difference equations for the total biomass of each population and that conservation of total nutrient allows a further reduction to a limiting system where the nutrient is effectively eliminated. The global dynamics and chain transitive sets of the resulting limiting system are analyzed. In Section 4.3 we prove that competitive exclusion holds for the full size-structured system. The winner is the population able to grow at the lowest nutrient concentration.

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4.1 The Model

In order to formulate a discrete, size-structured model of m-species competition for a limiting nutrient in a chemostat, a simple open system with a constant input of fresh nutrient at concentration $S^0 \in (0,\infty)$ at rate $E \in (0,1)$ and a constant removal of nutrient and organisms at rate E, we make the following biological assumptions (see Gage et al. [127]):

(1) An organism approximately doubles in size as it moves from its smallest to its largest size class;
(2) Cells divide into two daughter cells of approximately equal size;
(3) Cell growth is exponential if the concentration of the limiting nutrient remains constant;
(4) The average nutrient uptake rate per unit biomass is constant across all size classes;
(5) Respiration and mortality are negligible;
(6) Washout is constant across all size classes per unit biomass;
(7) The only organism-to-organism interaction is mediated through the nutrient concentration.

For the ith species we choose r_i size classes such that the average biomass in class j, $1 \le j \le r_i$, is $M_i^{j-1}b_i$, where $M_i = 2^{1/r_i}$ and b_i is the average biomass of a newly divided cell. Let $x^i = (y_i^1, y_i^2, \ldots, y_i^{r_i}) \in \mathbb{R}^{r_i}$, where y_i^j denotes the biomass in size class j, $1 \le j \le r_i$. Then the number of cells in size class j is $n_i(j) = y_i^j/(M_i^{j-1}b_i)$. Let S be the nutrient concentration, and $f_i(S)$ the nutrient uptake rate computed per unit biomass per iteration period. It is assumed that population biomass is measured in nutrient-equivalent units so that $f_i(S)$ is also the rate of increase in biomass per iteration period per unit biomass. Thus $y_i^j f_i(S)/(M_i^j b_i - M_i^{j-1}b_i) = n_i(j)f_i(S)(M_i-1)^{-1}$ is the number of individuals in size class j that can gain enough biomass during an iteration period to move up to size class $j+1$, and hence $P_i = f_i(S)(M_i-1)^{-1}$ is the proportion of individuals that would move from size class j to size class $j+1$ per iteration period in the absence of washout. Accounting for the ratio M_i of cell size in class $j+1$ to cell size in class j and the washout rate E, the proportion of biomass in class j projected into class $j+1$ over an iteration period is $(1-E)M_iP_i$. The proportion $(1-E)(1-P_i)$ of individuals remains in class j.

The discrete-time, size-structured model of m-species competition in the chemostat is then given by

$$\begin{aligned} x_{n+1}^i &= A_i(S_n)x_n^i, \qquad 1 \le i \le m, \\ S_{n+1} &= (1-E)\left(S_n - \sum_{j=1}^{m} f_j(S_n)U_n^j\right) + ES^0, \end{aligned} \tag{4.1}$$

where the vector $x_n^i \in \mathbb{R}_+^{r_i}$, $r_i > 0$, gives the distribution of biomass (in nutrient-equivalent units) of the ith microbial population among r_i size classes at the nth time step, and S_n is the nutrient concentration at the nth time step. The total biomass of the ith population at the nth time step is given by $U_n^i = x_n^i \cdot \mathbf{1}$, the scalar product of x_n^i and $\mathbf{1} = (1, \ldots, 1) \in \mathbb{R}^{r_i}$. The nutrient uptake rate for the ith population is $f_i(S)$, and the $r_i \times r_i$ projection matrix for that population is given by

$$A_i(S) = (1-E)\begin{bmatrix} 1-P_i & 0 & \cdots & & & M_iP_i \\ M_iP_i & 1-P_i & 0 & \cdots & & 0 \\ 0 & M_iP_i & 1-P_i & 0 & \cdots & 0 \\ & & \ddots & & & \\ 0 & \cdots & & 0 & M_iP_i & 1-P_i \end{bmatrix}, \tag{4.2}$$

where

$$M_i = 2^{1/r_i}, \quad P_i = f_i(S)(M_i - 1)^{-1}, \quad 1 \le i \le m.$$

Throughout this chapter, we assume that

(H1) For each $1 \le i \le m$, $f_i \in C^1(\mathbb{R}_+, \mathbb{R}), f_i(0) = 0, f_i'(S) > 0, f_i'(S) \le f_i'(0)$, $S \in \mathbb{R}_+$;

(H2) $f_i(+\infty)(M_i - 1)^{-1} < 1$, $1 \le i \le m$, and there exist $W > S^0$ and $\eta \in (0,1)$ such that $W \sum_{i=1}^m f_i'(0) < \eta$.

Clearly, (H1) and the mean value theorem imply that $f_i(S) \le f_i'(0)S$, for $S \ge 0$. The prototypical nutrient uptake rate, which satisfies (H1), is the Michaelis–Menten function

$$f(S) = \frac{mS}{a+S}, \qquad S \in \mathbb{R}_+,$$

where m is the maximum uptake rate and $a > 0$ is the Michaelis-Menten (or half saturation) constant. In (H2), W is an appropriate upper bound on the total biomass of all species and the nutrient, and η an acceptable tolerance. We refer to [327] for a discussion of subtle issues involving the time step and growth rates in order that the model make biological sense.

Using the fact that $\mathbf{1} = (1, \ldots, 1) \in \mathbb{R}^{r_i}$ is the Perron–Frobenius (principal) eigenvector of the nonnegative, irreducible, and primitive matrix $A_i(S)$ associated with its Perron–Frobenius (principal) eigenvalue $(1-E)(1+f_i(S))$ (see, e.g., [77, Theorem 1.1.1]), it follows that the total biomass $U_n^i = x_n^i \cdot \mathbf{1}$ satisfies the difference equations

$$U_{n+1}^i = (1-E)(1+f_i(S_n))U_n^i, \quad 1 \le i \le m. \tag{4.3}$$

Let $\Sigma_n = S_n + \sum_{i=1}^m U_n^i$, $n \ge 0$. Equation (4.3) and the second equation of (4.1) imply that the evolution of Σ_n can be decoupled from the rest of the system

$$\Sigma_{n+1} = (1-E)\Sigma_n + ES^0, \quad n \ge 0, \tag{4.4}$$

resulting in

$$\Sigma_n = S^0 - (1-E)^n(S^0 - \Sigma_0), \quad n \ge 0. \tag{4.5}$$

Clearly, (4.5) implies $\lim_{n\to\infty} \Sigma_n = S^0$, which is a conservation principle for the total nutrient.

4.2 The Limiting System

For the dynamics of system (4.1), we may consider its population level dynamics, which is described by equation (4.3) and the second equation in (4.1). In view of $S_n = \Sigma_n - \sum_{i=1}^m U_n^i$ and $\lim_{n\to\infty} \Sigma_n = S^0$, we may pass to the limiting system

$$U_{n+1}^i = (1-E)\left(1 + f_i(S^0 - \sum_{j=1}^m U_n^j)\right) U_n^i, \quad 1 \le i \le m, \tag{4.6}$$

with the initial value $(U_0^1, \dots, U_0^m)$ in the domain

$$D := \left\{(U^1, \dots, U^m) \in \mathbb{R}_+^m : \quad \sum_{i=1}^m U^i \le S^0\right\}.$$

Denote by F the mapping determined by the right side of (4.6), so we have

$$(U_{n+1}^1, \dots, U_{n+1}^m) = F(U_n^1, \dots, U_n^m).$$

Then the following result implies that D is positively invariant for system (4.6), and hence (4.6) defines a discrete dynamical system on D.

Lemma 4.2.1. *$F(D) \subset \left\{(U^1, \dots, U^m) \in \mathbb{R}_+^m : \quad \sum_{i=1}^m U^i \le (1-E)S^0\right\} \subset D$.*

Proof. For any $(U^1, \dots, U^m) \in D$, let $(V^1, \dots, V^m) = F(U^1, \dots, U^m)$ and $t = \sum_{i=1}^m U^i$. Then $V^i \ge 0$, $1 \le i \le m$, and $t \in [0, S^0]$. If $t > 0$, then

$$\begin{aligned}\sum_{i=1}^m V^i &= (1-E)t\left(1 + \sum_{i=1}^m f_i(S^0 - t)\frac{U^i}{t}\right) \\ &\le (1-E)t\left(1 + \max_{1\le i\le m}\{f_i(S^0 - t)\}\right) \\ &\le (1-E)\max_{1\le i\le m}\{(1 + f_i(S^0 - t))t\}.\end{aligned} \tag{4.7}$$

By (H1) and (H2), we have

$$\begin{aligned}\frac{d}{dt}\big((1 + f_i(S^0 - t))t\big) &= 1 + f_i(S^0 - t) - f_i'(S^0 - t)t \\ &\ge 1 - f_i'(0)W + f_i(S^0 - t) > 1 - \eta > 0.\end{aligned} \tag{4.8}$$

Consequently, the function $(1 + f_i(S^0 - t))t$ is strictly increasing with respect to $t \in [0, S^0]$, attaining its maximum value S^0 at $t = S^0$. Thus (4.7) yields $\sum_{i=1}^m V^i \le (1-E)S^0$. ∎

We define the break-even nutrient concentration for ith population as the solution λ_i of

$$(1-E)(1+f_i(S))=1,$$

where $\lambda_i=+\infty$ if no such solution exists. If the supplied nutrient does not exceed the nutrient requirements of a population, then it is eliminated.

Lemma 4.2.2. *If $\lambda_i \geq S^0$, then $\lim_{n\to\infty} U_n^i = 0$ for every solution $(U_n^1,\ldots,U_n^m)$ of (4.6).*

Proof. $U_{n+1}^i \leq (1-E)(1+f_i(S^0-U_n^i))U_n^i \equiv g(U_n^i)$, so, since g is increasing by (4.8), $U_n^i \leq V_n^i$, where $V_{n+1}^i = g(V_n^i)$ and $V_0^i = U_0^i$. We show that $V_n^i \to 0$. Our hypothesis ensures that $(1-E)(1+f_i(S^0-U))<1$ if $U\in(0,S^0]$, so $g(U)<U$ for $U\in(0,S^0]$. Consequently, $V_{n+1}^i < V_n^i$ if $V_0^i>0$, so V_n^i converges to the only fixed point of g, namely, zero. ∎

In view of (4.3), the biomass of a population can grow at a lower nutrient concentration than the biomass of the other populations, and consequently, we expect that the population with the lowest nutrient concentration is the superior competitor. The following result on the global dynamics of system (4.6) is, therefore, plausible.

Theorem 4.2.1. *Assume that $\lambda_1 < S^0$, and $\lambda_1 < \lambda_i$ for all $i \geq 2$. Then for any $(U_0^1,\ldots,U_0^m)\in D$ with $U_0^1>0$, the solution of (4.6) satisfies*

$$\lim_{n\to\infty}(U_n^1,U_n^2,\ldots,U_n^m)=(S^0-\lambda_1,0,\ldots,0).$$

Proof. For any $(U^1,\ldots,U^m)\in D$, let $(V^1,\ldots,V^m)=F(U^1,\ldots,U^m)$. Define

$$D_1 := \left\{(U^1,\ldots,U^m)\in D: \quad \sum_{i=1}^m U^i \geq S^0-\lambda_1\right\}$$

and $W_1(U^1,\ldots,U^m)=\sum_{i=1}^m U^i$. If $(U^1,\ldots,U^m)\in D_1$, then for system (4.6),

$$\begin{aligned}
\dot{W}_1(U^1,\ldots,U^m) &:= W_1(F(U^1,\ldots,U^m))-W_1(U^1,\ldots,U^m)\\
&= \sum_{i=1}^m V^i - \sum_{i=1}^m U^i\\
&= \sum_{i=1}^m \left[(1-E)\left(1+f_i(S^0-\sum_{j=1}^m U^j)\right)-1\right]U^i\\
&\leq \sum_{i=1}^m \left[(1-E)(1+f_i(\lambda_1))-1\right]U^i\\
&= \sum_{i=2}^m \left[(1-E)(1+f_i(\lambda_1))-1\right]U^i \leq 0. \qquad (4.9)
\end{aligned}$$

Thus W_1 is a Liapunov function of (4.6) on D_1 (see Definition 1.1.1). By the fact that each term in large brackets in the third line of (4.9) is nonpositive in D_1, it follows that

$$\begin{aligned} E_1 &:= \{(U^1, \ldots, U^m) \in D_1 : \quad \dot{W}_1(U^1, \ldots, U^m) = 0\} \\ &= \{(S^0 - \lambda_1, 0, \ldots, 0)\}. \end{aligned} \tag{4.10}$$

Let $u_n = (U_n^1, \ldots, U_n^m)$ be the solution of (4.6) with $u_0 \in D$, and let $\omega(u_0)$ be the omega limit of the positive orbit $\gamma^+(u_0) := \{u_n; n \geq 0\}$. If $\gamma^+(u_0) \subset D_1$, then the LaSalle invariance principle (see Theorem 1.1.1) implies that $\omega(u_0) = (S^0 - \lambda_1, 0, \ldots, 0)$.

Define

$$D_2 := \left\{ (U^1, \ldots, U^m) \in \mathbb{R}_+^m : \quad \sum_{i=1}^m U^i \leq S^0 - \lambda_1 \right\}.$$

Clearly, $D_2 \subset D$. By (4.8), when $t = S^0 - \lambda_1$ the strictly increasing function $(1 + f_i(S^0 - t))t$ on $[0, S^0 - \lambda_1]$ attains its maximum value $(1 + f_i(\lambda_1))(S^0 - \lambda_1)$. Note that $(1 + f_i(\lambda_1)) \leq (1 + f_i(\lambda_i)) = 1/(1 - E)$, $1 \leq i \leq m$. Then (4.7) implies that $\sum_{i=1}^m V^i \leq S^0 - \lambda_1$. Thus $(V^1, \ldots, V^m) \in D_2$, and hence D_2 is positively invariant for system (4.6). Define $W_2(U^1, \ldots, U^m) = -U^1$. If $(U^1, \ldots, U^m) \in D_2$, then for system (4.6),

$$\begin{aligned} \dot{W}_2(U^1, \ldots, U^m) &:= W_2(F(U^1, \ldots, U^m)) - W_2(U^1, \ldots, U^m) \\ &= -V^1 - (-U^1) = U^1 - V^1 \\ &= U^1 - (1 - E)\left(1 + f_1\left(S^0 - \sum_{j=1}^m U^j\right)\right) U^1 \\ &\leq U^1 \left[1 - (1 - E)(1 + f_1(\lambda_1)\right] = 0. \end{aligned} \tag{4.11}$$

Thus W_2 is a Liapunov function of (4.6) on D_2. Let

$$L := \left\{ (U^1, \ldots, U^m) \in \mathbb{R}_+^m : \quad U^1 = 0, \sum_{i=1}^m U^i < S^0 - \lambda_1 \right\},$$

and

$$\varDelta := \left\{ (U^1, \ldots, U^m) \in \mathbb{R}_+^m : \quad \sum_{i=1}^m U^i = S^0 - \lambda_1 \right\}.$$

By (4.11), we then have

$$E_2 := \{(U^1, \ldots, U^m) \in D_2 : \quad \dot{W}_2(U^1, \ldots, U^m) = 0\} = L \cup \varDelta. \tag{4.12}$$

If $u_0 = (U_0^1, \ldots, U_0^m) \in D_2$ with $U_0^1 > 0$, then $\gamma^+(u_0) \subset D_2$. By the LaSalle invariance principle (see Theorem 1.1.1), $\omega(u_0) \subset L \cup \varDelta$. Note that $0 \geq$

$\dot{W}_2(u_n) = W_2(u_{n+1}) - W_2(u_n) = U_n^1 - U_{n+1}^1, \forall n \geq 0$. Then we get $U_{n+1}^1 \geq U_n^1, \forall n \geq 0$, and hence $U_n^1 \geq U_0^1 > 0, \forall n \geq 0$. Thus $\omega(u_0) \subset \mathit{\Delta}$. Clearly, (4.10) implies that for any $u \in \mathit{\Delta} \setminus \{(S^0 - \lambda_1, 0, \ldots, 0)\}$, we have $\dot{W}_1(u) < 0$, and hence

$$F(u) \subset \left\{ (U^1, \ldots, U^m) \in D : \quad \sum_{i=1}^m U^i < S^0 - \lambda_1 \right\}.$$

So $(S^0 - \lambda_1, 0, \ldots, 0)$ is the only invariant set in $\mathit{\Delta}$. Thus $\omega(u_0) = (S^0 - \lambda_1, 0, \ldots, 0)$.

For any $u_0 = (U_0^1, \ldots, U_0^m) \in D$ with $U_0^1 > 0$, let $u_n = (U_n^1, \ldots, U_n^1)$, $n \geq 0$, be the solution of (4.6). Clearly, $U_n^1 > 0, \forall n \geq 0$, and *either* $\gamma^+(u_0) \subset D_1$, *or* there is an $n_0 \geq 0$ such that $u_{n_0} \in D_2$. Note that $\omega(u_0) = \omega(u_{n_0})$. Then in either case, by what we have proved above, $\omega(u_0) = (S^0 - \lambda_1, 0, \ldots, 0)$, and hence $\lim_{n\to\infty} u_n = (S^0 - \lambda_1, 0, \ldots, 0)$. This completes the proof. ∎

Theorem 4.2.2. *Assume that* $\lambda_1 < \lambda_2 < \ldots < \lambda_m$. *Then every compact internally chain transitive set for* F *is a fixed point of* F *itself.*

Proof. Let $e_0 = \mathbf{0} \in \mathbb{R}^m$, and in the case that $\lambda_i < S^0$, let $e_i = (0, \ldots, 0, S^0 - \lambda_i, 0, \ldots, 0) \in \mathbb{R}^m$ with its ith component being $(S^0 - \lambda_i)$ and the others being 0. Clearly, all these e_i are fixed points of $F : D \to D$. For any $v_0 \in D$ with $v_0 \neq e_0$, there exists $1 \leq k \leq m$ such that $v_0 = (0, \ldots, 0, V_0^k, \ldots, V_0^m)$ with $V_0^k > 0$. Let $v_n = (V_n^1, \ldots, V_n^m)$ be the solution of (4.6). Clearly, $V_n^i = 0, \forall n \geq 0, 1 \leq i < k$. If $\lambda_k < S^0$, then Theorem 4.2.1 implies that $\lim_{n\to\infty} v_n = e_k$. If $\lambda_k \geq S^0$, then $\lambda_i \geq S^0, \forall i \geq k$, and hence Lemma 4.2.2 implies that $\lim_{n\to\infty} v_n = e_0$. This convergence result also implies that each e_i is an isolated invariant set in $D \subset \mathbb{R}^m$ for F, and that no subset of e_i's forms a cyclic chain in D. By a convergence theorem (see Theorem 1.2.2), any compact internally chain transitive set for F is a fixed point of F. ∎

4.3 Global Dynamics

In this section we first lift the result for the limiting system (4.6) to the reduced system at the total population level (see (4.13) below), and then consider the global dynamics of the full size-structured system (4.1).

The population level dynamics are described by

$$\begin{aligned} U_{n+1}^i =& (1-E)\left(1 + f_i(S_n)\right) U_n^i, \quad 1 \leq i \leq m, \\ S_{n+1} =& (1-E)\left(S_n - \sum_{j=1}^m f_j(S_n) U_n^j\right) + ES^0, \end{aligned} \tag{4.13}$$

with the initial value $(U_0^1, \ldots, U_0^m, S_0)$ in the domain

$$\mathit{\Omega} := \left\{ (U^1, \ldots, U^m, S) \in \mathbb{R}_+^{m+1} : \quad \sum_{i=1}^m U^i + S \leq W \right\}.$$

Denote by G the mapping determined by the right side of (4.13), so we have

$$(U^1_{n+1}, \dots, U^m_{n+1}, S_{n+1}) = G(U^1_n, \dots, U^m_n, S_n).$$

If $(U^1, \dots, U^m, S) \in \Omega$, then

$$S - \sum_{i=1}^{m} f_i(S)U^i \geq S\left(1 - \sum_{i=1}^{m} W f_i'(0)\right) > (1-\eta)S \geq 0.$$

By the conservation principle (4.4) and the fact that $S^0 < W$, it then follows that $G(U^1, \dots, U^m, S) \in \Omega$, and hence $G(\Omega) \subset \Omega$. Thus system (4.13) defines a discrete dynamical system on Ω. The following result describes the competitive exclusion dynamics of (4.13).

Theorem 4.3.1. *Assume that $\lambda_1 < S^0$ and $\lambda_1 < \lambda_2 < \dots < \lambda_m$. Then for any $(U^1_0, \dots, U^m_0, S_0) \in \Omega$ with $U^1_0 > 0$, the solution of (4.13) satisfies*

$$\lim_{n \to \infty} (U^1_n, U^2_n, \dots, U^m_n, S_n) = (S^0 - \lambda_1, 0, \dots, 0, \lambda_1).$$

Proof. Fix $(U^1_0, \dots, U^m_0, S_0) \in \Omega$ with $U^1_0 > 0$, and let $(U^1_n, \dots, U^m_n, S_n)$ be the solution of system (4.13). Clearly, $U^1_n > 0, \forall n \geq 0$. Let $\Sigma_n = S_n + \sum_{i=1}^m U^i_n$, $n \geq 0$. By (4.4), $u_n = (U^1_n, \dots, U^m_n, \Sigma_n)$ satisfies the following system

$$\begin{aligned} U^i_{n+1} &= (1-E)\left(1 + f_i(\Sigma_n - \sum_{j=1}^{m} U^j_n)\right)U^i_n, \quad 1 \leq i \leq m, \\ \Sigma_{n+1} &= (1-E)\Sigma_n + ES^0. \end{aligned} \tag{4.14}$$

Let $\omega = \omega(u_0)$ be the omega limit set of the positive orbit $\gamma^+(u_0)$ of (4.14). Then

$$\omega \subset \left\{(U^1, \dots, U^m, \Sigma) \in \mathbb{R}^{m+1}_+ : \quad \Sigma \leq W\right\}.$$

Note that $\Sigma_n - \sum_{i=1}^m U^i_n = S_n \geq 0$, $n \geq 0$, and $\lim_{n\to\infty} \Sigma_n = S^0$. It then follows that for any $(U^1, \dots, U^m, \Sigma) \in \omega$, we have $\sum_{i=1}^m U^i \leq \Sigma$ and $\Sigma = S^0$. Thus, there exists a set $\tilde{\omega} \subset D$ such that $\omega = \tilde{\omega} \times \{S^0\}$. Denote by H the mapping determined by the right side of (4.14), so $(U^1_{n+1}, \dots, U^m_{n+1}, \Sigma_{n+1}) = H(U^1_n, \dots, U^m_n, \Sigma_n)$. By Lemma 1.2.1, ω is a compact, invariant, and internally chain transitive set for H. Moreover,

$$H|_\omega(U^1, \dots, U^m, S^0) = \left(F(U^1, \dots, U^m), S^0\right).$$

It then follows that $\tilde{\omega}$ is a compact, invariant, and internally chain transitive set for $F : D \to D$. By Theorem 4.2.2, we get $\tilde{\omega} = e_l$ for some $0 \leq l \leq p$, where p is the maximal index such that $\lambda_p < S^0$, and hence, $\omega = \tilde{\omega} \times \{S^0\} = (e_l, S^0)$. Thus

$$\lim_{n \to \infty} u_n = \lim_{n \to \infty} (U^1_n, \dots, U^m_n, \Sigma_n) = (e_l, S^0). \tag{4.15}$$

It remains to prove that $l = 1$. Suppose, by contradiction, that $l \neq 1$. Define

$$\delta_l = \begin{cases} \frac{1}{2}\left(1 + (1-E)(1 + f_1(S^0))\right) & \text{if } l = 0, \\ \frac{1}{2}\left(1 + (1-E)(1 + f_1(\lambda_l))\right) & \text{if } l \geq 2. \end{cases}$$

Since $\lambda_1 < S^0$ and $\lambda_l > \lambda_1$ if $l \geq 2$, we have

$$1 < \delta_0 < (1-E)(1+f_1(S^0)), \text{ and } 1 < \delta_l < (1-E)(1+f_1(\lambda_l)) \text{ if } l \geq 2.$$

By (4.15), it follows that

$$\lim_{n\to\infty}(1-E)\left(1 + f_1\left(\Sigma_n - \sum_{j=1}^m U_n^j\right)\right) = (1-E)(1+f_1(\lambda_l)) \text{ if } l \geq 2,$$

and

$$\lim_{n\to\infty}(1-E)\left(1 + f_1\left(\Sigma_n - \sum_{j=1}^m U_n^j\right)\right) = (1-E)(1+f_1(S^0)) \text{ if } l = 0.$$

Then there is an $n_0 > 0$ such that

$$(1-E)\left(1 + f_1\left(\Sigma_n - \sum_{j=1}^m U_n^j\right)\right) > \delta_l, \quad \forall n \geq n_0,$$

and hence $U_{n+1}^1 \geq \delta_l U_n^1, \quad \forall n \geq n_0$. In view of the fact that $\delta_l > 1$ and $U_n^1 > 0$, $\forall n \geq 0$, we get $\lim_{n\to\infty} U_n^1 = +\infty$, which contradicts the boundedness of $\{U_n^1 : n \geq 0\}$. By (4.15), it then follows that $\lim_{n\to\infty}(U_n^1, \ldots, U_n^m, \Sigma_n) = (e_1, S^0)$, and hence

$$\lim_{n\to\infty}(U_n^1, \ldots, U^n, S_n) = (e_1, \lambda_1) = (S^0 - \lambda_1, 0, \ldots, 0, \lambda_1).$$

This completes the proof. ∎

To get the global dynamics of the full system (4.1), we need the following weak ergodic theorem of Golubitsky, Keeler and Rothschild (see [132, Corollary 3.2]).

Weak Ergodic Theorem *Suppose that T_k is a sequence of nonnegative, irreducible, and primitive $m \times m$ matrices and that $T_k \to T$ as $k \to \infty$, where T is also irreducible and primitive. If e is the Perron–Frobenius eigenvector of T satisfying $e \cdot \mathbf{1} = 1$, and $x_{k+1} = T_k x_k$ is a sequence starting with $x_0 \geq 0$ and $x_0 \neq 0$, then $\frac{x_k}{x_k \cdot \mathbf{1}} \to e$ as $k \to \infty$.*

Let $r = \sum_{i=1}^{m} r_i$ and set $\Gamma :=$

$$\left\{(x^1, \dots, x^m, S) \in \mathbb{R}_+^{r+1} : x^i \in \mathbb{R}^{r_i}, 1 \le i \le m, \text{ and } \sum_{i=1}^{m} x^i \cdot \mathbf{1} + S \le W\right\}.$$

Clearly, the positive invariance of Ω for (4.13) implies that of Γ for (4.1). So (4.1) defines a discrete dynamical system on Γ. The next result shows that the surviving population asymptotically approaches a stable, uniform size distribution.

Theorem 4.3.2. *Assume that $\lambda_1 < S^0$ and $\lambda_1 < \lambda_2 < \ldots < \lambda_m$. Then for any $(x_0^1, \dots, x_0^m, S_0) \in \Gamma$ with $x_0^1 \ne \mathbf{0}$, the solution of (4.1) satisfies*

$$\lim_{n\to\infty} (x_n^1, x_n^2, \dots, x_n^m, S_n) = \left(\frac{S^0 - \lambda_1}{r_1}\mathbf{1}, \mathbf{0}, \dots, \mathbf{0}, \lambda_1\right).$$

Proof. Given $(x_0^1, \dots, x_0^m, S_0) \in \Gamma$ with $x_0^1 \ne \mathbf{0}$, let $U_n^i = x_n^i \cdot \mathbf{1}, \forall 1 \le i \le m$, $n \ge 0$. Then $(U_0^1, \dots, U_0^m, S_0) \in \Omega$ with $U_0^1 > 0$. By Theorem 4.3.1, $\lim_{n\to\infty}(U_n^1, U_n^2, \dots, U_n^m, S_n) = (S^0 - \lambda_1, 0, \dots, 0, \lambda_1)$. Then $\lim_{n\to\infty} A_i(S_n) = A_i(\lambda_1)$, $1 \le i \le m$. As mentioned in Section 4.1, $A_i(S_n)$ and $A_i(\lambda_1)$ are nonnegative, irreducible, and primitive, and they have $e = \frac{1}{r_i}\mathbf{1}$ as their Perron–Frobenius eigenvectors with $e \cdot \mathbf{1} = 1$. By the aforementioned weak ergodic theorem, we then have

$$\lim_{n\to\infty} \frac{x_n^i}{x_n^i \cdot \mathbf{1}} = \lim_{n\to\infty} \frac{x_n^i}{U_n^i} = e = \frac{1}{r_i}\mathbf{1}, \quad \forall 1 \le i \le m.$$

Since $\lim_{n\to\infty} U_n^1 = S^0 - \lambda_1$ and $\lim_{n\to\infty} U_n^i = 0$, $\forall 2 \le i \le m$, we conclude that

$$\lim_{n\to\infty} (x_n^1, x_n^2, \dots, x_n^m, S_n) = \left(\frac{S^0 - \lambda_1}{r_1}\mathbf{1}, \mathbf{0}, \dots, \mathbf{0}, \lambda_1\right).$$

This completes the proof. ∎

4.4 Notes

The model (4.1) was formulated by Gage, Williams and Horton [127] and was further developed by Smith [327]. This chapter is adapted from Smith and Zhao [339]. The proof of Theorem 4.2.1 was motivated by a similar LaSalle invariance principle argument in Armstrong and McGehee [18] for the classical chemostat system of ordinary differential equations. Theorems 4.2.1, 4.3.1, and 4.3.2 were proved for the case of two-species competition in [327], where monotonicity and Butler–McGehee lemma arguments were applied. Recently, Arino, Gouzé and Sciandra [17] extended the model (4.1) with $m = 1$ to the case where cell division (and consequently, cell birth) can happen for cells in several biomass classes, the effective size at division being distributed following some probability density, and showed that the model system admits one nonzero globally stable equilibrium. There have been extensive investigations on both discrete and continuous structured population models; see, e.g., Cushing [77] and the references therein.