A Mathematical Model of the Chemostat with a General Class of Functions Describing Nutrient Uptake

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A MATHEMATICAL MODEL OF THE CHEMOSTAT WITH A GENERAL CLASS OF FUNCTIONS DESCRIBING NUTRIENT UPTAKE*

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Abstract. A model of the chemostat involving n microorganisms competing for a single essential, growth-limiting substrate is considered. Instead of assuming the familiar Michaelis–Menten kinetics for nutrient uptake, a general class of functions is used which includes all monotone increasing uptake functions, but which also allows uptake functions that describe inhibition by the substrate at high concentrations.

The qualitative behaviour of this generalized model is determined analytically. It is shown that the behaviour depends intimately upon certain parameters. Provided that all the parameters are distinct (which is a biologically reaonable assumption), at most one competitor survives. The substrate and the surviving competitor (if one exists), approach limiting values. Thus there is competitive exclusion. However, unlike the standard model, in certain cases the outcome is initial condition dependent.

1. Introduction. The chemostat is a laboratory apparatus used for the continuous culture of microorganisms. It can be used to study competition between different populations of microorganisms for a growth-limiting substrate, and has the advantage that certain of the biological parameters presumed to influence competitive outcome can be controlled by the experimenter. In this paper we consider a deterministic model of purely exploitative competition between n populations of microorganisms for a single, essential, growth-limiting nutrient, in a chemostat with constant input and wash-out rate. Our purpose is to show that for any "realistic" functions describing nutrient uptake rates for the competing microorganisms, the principle of competitive exclusion holds. That is to say, at most one population of microorganisms survives. Furthermore, the system always asymptotically approaches an equilibrium state. Our results may be regarded as extending those of Hsu, Hubbell and Waltman [16] and a result of Armstrong and McGehee [3]. The novelty of this work is that in allowing very general nutrient-uptake functional responses, the competitive outcome becomes, in some cases, initial condition dependent. This is in contrast to the references cited above, but has been noted experimentally and by numerical simulation in the case of nutrient inhibition [1], [25], [30], of which we give a brief discussion later. For a more detailed account of the chemostat and related experimental results, we refer the reader to [11], [16], [17], [21], [23], [24], [29].

This paper is organized in the following manner. In § 2 we present the model and some background remarks. Section 3 contains a statement of the main results. However, for clarity of presentation, the proofs of these results are deferred to § 5. Proofs of the preliminary results and technical lemmas are given in § 4. We conclude with a discussion and an application in § 6.

2. The model. We shall consider the following model of the chemostat:

$$S'(t) = (S^0 - S(t))D - \sum_{i=1}^{n} \frac{x_i(t)p_i(S(t))}{y_i},$$

(2.1)
$$x_i'(t) = x_i(t)(-D + p_i(S(t))), \qquad i \in I,$$

$$S(0) = S_0 \geqq 0, \quad x_i(0) = x_{i0} > 0, \quad i \in I,$$

where $I = \{1, \cdots, n\}$.

In these equations, $x_i(t)$ denotes the concentration of the ith population of microorganisms at time t; $S(t)$ denotes the concentration of substrate at time t; $p_i(S)$ is the function that represents the rate of conversion of nutrient to biomass, i.e. the per capita growth rate of the ith population as a function of substrate concentration; y_i is a growth yield constant, and we assume $p_i(S)/y_i$ represents the substrate-uptake function for the ith population; S^0 denotes the concentration of substrate in the feed bottle; D denotes the input rate from the feed bottle containing the substrate and the wash-out rate of substrate, microorganisms and byproducts from the growth chamber. Thus $S^0 D$ represents the input rate of substrate concentration.

The system (2.1) describes a chemostat in which n populations of microorganisms compete exploitatively for a single, essential, growth-limiting substrate. It is assumed that the substrate is nonreproducing, the input concentration and the dilution rate are constant, and there is perfect mixing in the growth vessel so that substrate and microorganisms are removed in proportion to their concentrations. The individual death rate of any species is considered insignificant compared to the dilution rate, and it is assumed that growth rates adjust instantaneously to changes in the concentration of substrate. Furthermore we assume that the substrate-uptake rate is proportional to the rate of conversion to biomass. To motivate the conditions that we shall place on the uptake functions $p_i(S)$, we give a brief account of the development of the model.

Volterra, in 1928 [28], appears to have been the first to use a mathematical model to show that under certain conditions, the coexistence of two or more populations competing for the same limiting resource is impossible. In his model, he assumed a linear relationship between the amount of substrate present and the specific growth rate for each of the competing populations; in the context of (2.1) this requires the functions $p_i(S)$ to be linear functions. Monod, in 1942 [21], formulated a model which featured the dependence of microbial growth rate on the concentration of the limiting substrate, as a data-fitting curve which later was interpreted in terms of Michaelis–Menten kinetics. A theoretical derivation of the same model involving a substrate and a single population is given, for example, in [13]. An extension of this basic model to several competing populations was given by Taylor and Williams [27]. In these models there is a saturation effect at higher resource levels; $p_i(S)$ takes the form $m_i S/(a_i + S)$, where m_i and a_i are positive constants. A complete global analysis of this model was given by Hsu, Hubbell and Waltman [16] and Hsu [15]. They showed that at most one of the competing populations survives, the one whose "Michaelis–Menten constant" a_i, is smallest in comparison with its intrinsic growth rate, and that the dynamical system has an equilibrium point which is globally stable for solutions with positive initial conditions. This result was confirmed experimentally by Hansen and Hubbell [11]. Armstrong and McGehee [3] extended these theoretical results to models with arbitrary, smooth, monotone increasing uptake functions $p_i(S)$. An example of such functions is given by the Holling type III multiple saturation response of the form $p_i(S) = m_i S^2/(b_i + S)(c_i + S)$, see [17].

A number of authors have pointed out that certain substrates may be growth-limiting at low concentrations and growth-inhibiting at high concentrations; for example there is inhibition of Nitrobacter by nitrite and of Nitrosomonas by ammonia [17]. This results in nonmonotone uptake functions. Andrews [1] and Yang and Humphrey [30] discuss several specific models of inhibitory kinetics. Bush and Cook [5] give an analysis of such a model involving one substrate and one population of microorganisms, using a general inhibition function. Aris and Humphrey [2] give an analysis of a model of one substrate and two competing microorganisms, using a specific functional form of inhibitory kinetics proposed by Boon and Laudelout [4],

$$p_i(S) = m_i \Big/ \left(1 + \frac{b_i}{S} + \frac{S}{c_i}\right).$$

With inhibitory kinetics, each competing population of microorganisms has a lower threshold level of substrate below which it cannot grow (irrespective of competition) and an upper threshold level of substrate above which substrate inhibition prevents growth.

Guided by this, we make the following assumptions concerning the functions p_i in our model equations (2.1):

(2.2) $p_i : \mathbb{R}^+ \to \mathbb{R}^+$;

(2.3) p_i is continuously differentiable;

(2.4) $p_i(0) = 0$;

and there exist uniquely defined positive extended real
numbers λ_i and μ_i, with $\lambda_i \leqq \mu_i$, such that

$$p_i(S) < D \quad \text{if } S \notin [\lambda_i, \mu_i],$$

(2.5)   and

$$p_i(S) > D \quad \text{if } S \in (\lambda_i, \mu_i).$$

With inhibition kinetics in mind, λ_i and μ_i represent the break-even concentrations of substrate referred to above. But it should be noted that we allow λ_i and/or μ_i to be equal to $+\infty$ so that our results also apply in the case of any monotone uptake functions and in particular, in the case of Michaelis–Menten kinetics.

It will be evident from the method of proof that we could consider an even more general class of functions p_i; it is partly for the sake of clarity of our arguments and partly for the sake of biological reality that we impose conditions (2.2)–(2.5) above. Again, for the sake of clarity, we make two further assumptions of a generic nature:

(2.6)   if λ_i (or μ_i) is finite, then $p_i'(\lambda_i) \neq 0 (p_i'(\mu_i) \neq 0)$;

(2.7)   all λ_i, μ_j (other than those which are infinite) are distinct from each other and from S^0.

Note that in the definition of (2.1), we assume $x_{i0} > 0$ for all $i \in I$. This involves no loss of generality since if $x_{i0} = 0$ for some $i \in I$, then $x_i(t) = 0$ for all $t \geqq 0$ and that population can be eliminated from consideration.

3. Statement of results. From now on (except in Theorem 3.6 where we relax (2.7)), we assume that the functions p_i satisfy (2.2)–(2.7). First we note that (2.1) has positive, bounded solutions, which is a prerequisite for any reasonable model of the chemostat.

THEOREM 3.1. *All solutions* $S(t)$, $x_i(t)$, $i \in I$, *of* (2.1) *are positive and bounded for* $t > 0$.

The next result concerns competition-independent extinction of a population. It states that if the conversion rate of the ith organism is less than the dilution rate, for all nutrient densities below the input concentration, then that organism dies out.

THEOREM 3.2. *If* $\lambda_i \geqq S^0$ (*or* $\lambda_i = +\infty$), *then* $\lim_{t \to \infty} x_i(t) = 0$ *for all solutions of* (2.1).

Henceforth, we shall assume that the populations are labelled so that

$$(3.1) \qquad \lambda_1 < \lambda_2 < \cdots < \lambda_\nu < S^0 \leqq \lambda_j, \qquad \nu + 1 \leqq j \leqq n,$$

where $0 \leqq \nu \leqq n$. As a consequence of Theorem 3.2, x_1 through x_ν are the only competitors that have a chance of surviving. If $\nu = 0$, the system clearly crashes, i.e. all populations of microorganisms become extinct and the substrate concentration converges to S^0.

To describe our results on the competitive outcomes of the system (2.1), the following definitions will be useful.

Let $Q = \bigcup_{i=1}^{\nu} (\lambda_i, \mu_i)$. (If $\nu = 0$, let $Q = \varnothing$.)

From (2.7) and (3.1) it follows that every connected component of Q is an open interval of the form (λ_i, μ_k), where $1 \leqq i \leqq k$. Evidently, for each j, $1 \leqq j \leqq \nu$, λ_j and μ_j belong to the closure of exactly one and the same component of Q. Note that if (λ_i, μ_k) is a component of Q, then for any time τ for which $S(\tau) \in (\lambda_i, \mu_k)$, the concentration of at least one population of microorganisms is increasing.

Now we define

$$(3.2) \qquad \Gamma = \{\lambda_i : \lambda_i < S^0\} \cup \{\mu_j : \mu_j < S^0\}.$$

It will be convenient to relabel the elements of Γ as $\gamma_1 < \gamma_2 < \cdots < \gamma_k$. Note that $k \leqq 2\nu$.

The following results show that solutions of (2.1) always have limiting behaviour.

THEOREM 3.3. (a) *For any solution of* (2.1), $\lim_{t \to \infty} S(t) = \gamma$, *where* γ *is either* S^0 *or is the endpoint of a component of* Q.

(b) *A necessary condition for* $\lim_{t \to \infty} S(t) = \gamma$, *where* γ *is the endpoint of a component of* Q, *is that* $\gamma \leqq S^0$. *If* $\lim_{t \to \infty} S(t) = \gamma$, *where* γ *is such an endpoint, then* $\lim_{t \to \infty} x_i(t) = y_i(S^0 - \gamma)$ *if* $\gamma = \lambda_i$ *or* μ_i, *and* $\lim_{t \to \infty} x_j(t) = 0$ *for all other* j.

(c) *A necessary condition for* $\lim_{t \to \infty} S(t) = S^0$ *is that* $S^0 \notin Q$. *If* $\lim_{t \to \infty} S(t) = S^0$, *then* $\lim_{t \to \infty} x_i(t) = 0$ *for all* i.

In fact, for almost all solutions of (2.1), $\lim_{t \to \infty} S(t) = S^0$ or λ_i, where λ_i is the left endpoint of a component of Q. More precisely, we have the following theorem, which is the main result of this paper:

THEOREM 3.4. *Let* Λ *denote the set of left endpoints of components of* Q, *together with* S^0, *if* $S^0 \notin Q$. *With the exception of a set of initial conditions of Lebesgue measure zero, all solutions of* (2.1) *satisfy*

$$(3.3) \qquad \lim_{t \to \infty} S(t) = \gamma, \qquad \gamma \in \Lambda$$

with the corresponding asymptotic behaviour: $\lim_{t \to \infty} x_i(t) = y_i(S^0 - \lambda_i)$, $\lim_{t \to \infty} x_j(t) = 0$, $j \neq i$, *if* $\gamma = \lambda_i$; *and* $\lim_{t \to \infty} x_j(t) = 0$, $j \in I$ *if* $\gamma = S^0$.

Conversely, for each $\gamma \in \Lambda$, there is an open, nonempty set of initial conditions for which the solutions of (2.1) satisfy (3.3).

COROLLARY 3.5. *If* Q *is connected, then for all* $j \geqq 2$ $\lim_{t \to \infty} x_j(t) = 0$. *If, in addition,* $S^0 \in Q$, *then the critical point* $(\lambda_1, y_1(S^0 - \lambda_1), 0, \cdots, 0)$ *is globally asymptotically stable for* (2.1).

Corollary 3.5 applies to all models for which the functions p_i are monotonically increasing (actually only p_1 need be monotonically increasing), as well as those for which either the input concentration or the wash-out rate is sufficiently small.

The exceptional set mentioned in the statement of the above theorem consists of the stable manifolds of the (unstable) critical points $(S, x_1, \cdots, x_n)$ where $S = \mu_k$, $x_k = y_k(S^0 - \mu_k)$, $x_j = 0, j \neq k$; and μ_k is a right endpoint of a component of Q.

In all cases then, at most one competitor survives and the substrate and surviving competitor approach limiting values. Competitive exclusion therefore applies with the proviso that the outcome of the competition may be initial condition dependent.

If for the moment, we relax the generic assumption (2.7), i.e. no longer require that all λ_i and μ_j's be distinct from each other and from S^0, coexistence is possible (at least in a weak sense) as is suggested by the following theorem.

THEOREM 3.6. *For any solution of* (2.1), $\lim_{t \to \infty} S(t) = \gamma$ *where either* $\gamma = S^0$ *or* γ *is the endpoint of a component of* Q. *If* $\gamma = S^0$, *then* $\lim_{t \to \infty} x_j(t) = 0$, $j \in I$. *Otherwise* $\lim_{t \to \infty} (\sum_{i \in \Phi} x_i(t)/y_i) = S^0 - \gamma$ *where* $\Phi = \{i: \lambda_i = \gamma \text{ or } \mu_i = \gamma\}$, *and* $\lim_{t \to \infty} x_j(t) = 0$ *if neither* λ_j *nor* μ_j *is equal to* γ.

4. Lemmas and proofs of preliminary results.

Proof of Theorem 3.1. Let $z(t) = S(t) + \sum_{i=1}^{n} (x_i(t)/y_i)$. From (2.1), we have

$$(4.1) \qquad z'(t) = (S^0 - z(t))D$$

from which we obtain

$$(4.2) \qquad z(t) = S^0(1 - e^{-Dt}) + z_0 e^{-Dt}$$

where $z_0 = z(0)$. It is clear from (2.1) that the positive $(S, x_1, \cdots, x_n)$ cone is positively invariant. Thus solutions are positive for all $t > 0$ and so, by (4.2), are bounded.

The following corollary is immediate from (4.2).

COROLLARY 4.1. *The n-dimensional simplex,*

$$\mathcal{S} = \left\{ (S, x_1, \cdots, x_n): S, x_1, \cdots, x_n \geq 0; S + \sum_{i=1}^{n} \frac{x_i}{y_i} = S^0 \right\},$$

is a global attractor for (2.1).

Proof of Theorem 3.2. Let $(S(t), x_1(t), \cdots, x_n(t))$ be a solution of (2.1). Suppose that $S^0 \leq \lambda_i < \infty$. From Corollary 4.1 it follows that for each $\varepsilon > 0$, there exists $T = T(\varepsilon)$ such that

$$(4.3) \qquad S^0 - \frac{\varepsilon}{2y_i} \leq S(t) + \sum_{j=1}^{n} \frac{x_j(t)}{y_j} \leq S^0 + \frac{\varepsilon}{2y_i}, \qquad t \geq T(\varepsilon).$$

Since $p_i(S) - D < 0$ for $0 \leq S \leq S^0 - \varepsilon/2y_i$, we have $\delta_i = \max\{p_i(S) - D: 0 \leq S \leq S^0 - \varepsilon/2y_i\} < 0$. If $S(t) \geq S^0 - \varepsilon/2y_i$ for all sufficiently large t, then (4.3) implies that $x_i(t) \leq \varepsilon$ for all large t. If $S(t) \leq S^0 - \varepsilon/2y_i$ for all sufficiently large t, then we have $x_i'(t) \leq \delta_i x_i(t)$ for all large t, and again we shall have $x_i(t) \leq \varepsilon$ if t is large enough. If there is a sequence $t_n \to \infty$ with $S(t_n) = S^0 - \varepsilon/2y_i$, and

$$S(t) \begin{cases} \leq S^0 - \dfrac{\varepsilon}{2y_i}, & t_{2n} < t < t_{2n+1}, \\[2ex] \geq S^0 - \dfrac{\varepsilon}{2y_i}, & t_{2n+1} < t < t_{2n+2} \end{cases}$$

we have $x_i(t) \leqq \varepsilon$ on $[t_{2n+1}, t_{2n+2}]$ and $x_i'(t) < 0$ on (t_{2n}, t_{2n+1}), so $x_i(t) \leqq \varepsilon$ on (t_{2n}, t_{2n+1}), also. Thus in all cases, we have $x_i(t) \leqq \varepsilon$ for all sufficiently large t. It follows that $\lim_{t \to \infty} x_i(t) = 0$.

If $\lambda_i = \infty$, then $p_i(S) - D < 0$ for $0 \leqq S < \infty$. By Theorem 3.1 $S(t)$ is bounded above by σ, say and so $\eta_i = \max \{p_i(S) - D : 0 \leqq S \leqq \sigma\} < 0$. Since $0 \leqq S(t) \leqq \sigma$, for all t we have $x_i'(t) \leqq \eta_i x_i(t)$, and so $\lim_{t \to \infty} x_i(t) = 0$.

The following lemma describes a condition that guarantees convergence of the substrate to one of the break-even concentrations. An analogous result was proved in [16], based on a result of R. Miller [20]. Since the proof of our lemma is similar, we shall omit it.

LEMMA 4.2. *Let* $(S(t), x_1(t), \cdots, x_n(t))$ *be a solution of* (2.1). *Suppose that for some* i, $x_i(t)$ *converges monotonely to* $x_i^* > 0$ *as* $t \to \infty$. *Then* $\lim_{t \to \infty} S(t)$ *exists and is equal either to* λ_i *or to* μ_i.

In the event that $S(t)$ converges to a limit as $t \to \infty$, then it must be to S^0 or to one of the break-even concentrations, and the population biomasses have appropriate limiting behaviours. This is the content of the next lemma.

LEMMA 4.3. *Let* $(S(t), x_1(t), \cdots, x_n(t))$ *be a solution of* (2.1). *Suppose that* $\lim_{t \to \infty} S(t) = \gamma$. *Then*

(a) $\gamma = S^0$ *or is the endpoint of a component of* Q.

(b) *If* $\gamma = S^0$, *then* $\lim_{t \to \infty} x_i(t) = 0$, $i \in I$.

(c) *If* $\gamma = \lambda_i$ *or* μ_i, *the endpoint of a component of* Q, *then* $\lim_{t \to \infty} x_i(t) = y_i(S^0 - \gamma)$, $\lim_{t \to \infty} x_j(t) = 0$, $j \neq i$.

Proof. (a) From Corollary 4.1, we know that $0 < \gamma \leqq S^0$. Suppose that (a) does not hold. Then either $\gamma \in (\lambda_i, \mu_i)$ for some i, or there exists $\varepsilon_0 > 0$ such that $[\gamma - \varepsilon_0, \gamma + \varepsilon_0]$ is disjoint from $\bar{Q}$ (closure of Q).

In the former case, $\lambda_i < S(t) < \mu_i$ for t sufficiently large, which implies x_i is monotone increasing. By Lemma 4.2, it follows that $\lim_{t \to \infty} S(t)$ is equal either to λ_i or μ_i, contradicting $\gamma \in (\lambda_i, \mu_i)$.

In the latter case, we shall have $p_i(S(t)) - D < 0$ for all large t, for all i, so all the $x_i(t)$ are eventually monotone decreasing. If they all decrease to zero, then we have $\lim_{t \to \infty} S(t) = S^0$ by Corollary 4.1; otherwise we may apply Lemma 4.2 and deduce that $\lim_{t \to \infty} S(t) = \lambda_j$ or μ_j for some j. But this contradicts $[\gamma - \varepsilon_0, \gamma + \varepsilon_0] \cap \bar{Q} = \varnothing$. Thus (a) must hold.

(b) Follows at once from Corollary 4.1.

(c) If $\gamma = \lambda_i$ or μ_i, the endpoint of a component of Q, then for all $j \neq i$, we have $x_j'(t) < 0$ for t sufficiently large. If we had $\lim_{t \to \infty} x_j(t) > 0$, then $\lim_{t \to \infty} S(t) = \lambda_j$ or μ_j by Lemma 4.2, which is a contradiction. Thus $\lim_{t \to \infty} x_j(t) = 0$ for all $j \neq i$. That $\lim_{t \to \infty} x_i(t) = y_i(S^0 - \gamma)$ now follows from Corollary 4.1.

Recall that the simplex, $\mathscr{S} = \{(S, x_1, \cdots, x_n) : S, x_1, \cdots, x_n \geqq 0; S + \sum_{i=1}^n x_i/y_i = S^0\}$ is globally attracting for the system (2.1) (and therefore positively invariant). Since every bounded trajectory is asymptotic to its omega-limit set, it is evident that the dynamics of (2.1) restricted to $\mathscr{S}$ will provide the key to understanding the general behaviour of (2.1). It will be convenient to introduce the following notation for the positively invariant subsimplices of $\mathscr{S}$:

$$\mathscr{S}_H = \{(S, x_1, \cdots, x_n) \in \mathscr{S} : x_h > 0 \text{ if and only if } h \in H\}$$

defined for every subset H of I. Note then that $\mathscr{S} = \mathscr{S}_I$. Accordingly we denote the

system (2.1) restricted to these subsimplices as:

$$S'(t) = (S^0 - S(t))D - \sum_{i=1}^{n} \frac{x_i(t)}{y_i} p_i(S(t)),$$

(2.1)$_{\mathscr{S}_H}$

$$x_i'(t) = x_i(t)(-D + p_i(S(t))), \qquad i \in I,$$

$$S(0) = S_0 \geqq 0, \quad x_i(0) = x_{i0} > 0, \qquad i \in H, \quad x_{i0} = 0, \quad i \notin H.$$

$$S_0 + \sum_{i=1}^{n} \frac{x_{i0}}{y_i} = S^0.$$

We also define $Q_H = (\cup_{h \in H} (\lambda_h, \mu_h)) \cap Q$, the analogue of Q with respect to (2.1)$_{\mathscr{S}_H}$.
Note that solutions of (2.1)$_{\mathscr{S}}$ are positive for all $t > 0$ and satisfy,

(4.4) $$S'(t) + \sum_{i=1}^{n} \frac{x_i'(t)}{y_i} = 0, \qquad t > 0.$$

The next sequence of lemmas is directed at analysing (2.1)$_{\mathscr{S}}$.

We will be mainly concerned with showing that on the positively invariant linear manifold $\mathscr{S}$, the concentration of substrate, $S(t)$, eventually becomes trapped either outside of Q or inside a component of Q between particular values of Γ, forcing monotonic convergence of the concentration of each competitor, $x_i(t)$, and hence convergence of $S(t)$.

LEMMA 4.4. *Let* $(S(t), x_1(t), \cdots, x_n(t))$ *be a solution of* (2.1)$_{\mathscr{S}}$. *Let* γ *be the endpoint of a component of* Q. *Suppose there exists* $\tau \geqq 0$ *with* $S(\tau) = \gamma$. *Then* $S'(\tau) > 0$ *or* $n = 1$ *and* $S'(\tau) = 0$.

Proof. Since γ is the endpoint of a component of Q, $x_i'(\tau) = 0$ for some i and $x_j'(\tau) < 0$ for all $j \neq i$. The result now follows from (4.4).

The following lemma is an immediate consequence of Lemma 4.4.

LEMMA 4.5. *Let* $(S(t), x_1(t), \cdots, x_n(t))$ *be a solution of* (2.1)$_{\mathscr{S}}$ *and let* (λ_i, μ_j) *be a component of* Q. *Then, for all sufficiently large* t, *precisely one of the following occurs*:

(a) $S(t) < \lambda_i$, *or*

(b) $\lambda_i \leqq S(t) \leqq \mu_j$, *or*

(c) $S(t) > \mu_j$.

At this point we digress by stating and proving a result for the system (2.1). We do this here, to emphasize that in this special case the proof is fairly straightforward. However, the result is quite general and natural from a biological viewpoint. It states that if the competitor with the lowest break-even concentration level λ_1, also has its largest break-even concentration level μ_1 (level above which it is inhibited) greater than the input concentration rate S^0, then there is a globally asymptotically stable critical point. This applies in the case that $\mu_1 = +\infty$ and so it generalizes results of Hsu, Hubbell and Waltman [16]. More generally, it applies to all models in which the kinetic growth function p_1 is monotonically increasing.

THEOREM 4.6. *If* $\lambda_1 < S^0 < \mu_1$, *then the critical point* $E_{\lambda_1} = (\lambda_1, y_1(S^0 - \lambda_1), 0, \cdots, 0)$ *is globally asymptotically stable for* (2.1).

Proof. First we show that the result holds for (2.1)$_{\mathscr{S}_H}$ where $H = I \backslash \Theta$ and Θ is any index set such that $\Theta \subset I \backslash \{1\}$. By Lemma 4.4, if there exists $\tau \geqq 0$ such that $S(\tau) = \lambda_1$, then $S'(\tau) > 0$. (In the case that $n = 1$, $S'(\tau) = 0$ and $S(t) \equiv \lambda_1$.) Therefore, on $\mathscr{S}_H$, either $S(t) < \lambda_1$ for all $t \geqq 0$ or $\lambda_1 \leqq S(t) \leqq S^0$ for all large t. In the former case all $x_i(t)$ monotonely decrease. By (4.4), $S(t)$ must monotonely increase. Since $S(t)$ is bounded above, it converges and so the result follows by Lemma 4.3(a) and (c). In the latter

case, $x_1(t)$ is bounded above and monotonely increasing. Since this implies that it must converge to a positive limit, the result follows for $(2.1)_{\mathscr{S}_H}$, by Lemmas 4.2 and 4.3(a) and (c).

To show that the result holds for (2.1), it suffices to show that E_{λ_1} belongs to the omega-limit set, Ω, of any solution $(S(t), x_1(t), \cdots, x_n(t))$ of (2.1), since it is easily verified that E_{λ_1} is locally asymptotically stable for (2.1).

First we show that if $\overline{\lim}_{t\to\infty} x_1(t) > 0$, then $E_{\lambda_1} \in \Omega$. Suppose $\overline{\lim}_{t\to\infty} x_1(t) > 0$. Then there exists $P = (S, \xi_1, \cdots, \xi_n) \in \Omega$ with $\xi_1 > 0$. By Corollary 4.1, $P \in H$, for some $H \subset I$ with $1 \in H$, and so by the proof for $(2.1)_{\mathscr{S}_H}$ above, E_{λ_1} belongs to the closure of the orbit through P and hence belongs to Ω.

If we assume $\overline{\lim}_{t\to\infty} x_1(t) = 0$, and hence $\lim_{t\to\infty} x_1(t) = 0$, we derive a contradiction as follows. Let $z(t) = S(t) + \sum_{i=1}^{n} x_i(t)/y_i$. By (4.2), $\Omega \subset \mathscr{S}$, $\lim_{t\to\infty} z(t) = S^0$ and $\lim_{t\to\infty} z'(t) = 0$. In this case $\underline{\lim}_{t\to\infty} S(t) \leqq \lambda_1$ (or $x_1(t)$ increases to a positive limit) and so there exists $t_k \to \infty$ such that for fixed $\bar{\lambda}$ satisfying $\lambda_1 < \bar{\lambda} < \min(\lambda_2, S^0)$, $S(t_k) \leqq \bar{\lambda}$ and $\lim_{k\to\infty} S'(t_k) = 0$. Now $x_1'(t_k) = (-D + p_1(S(t_k)))x_1(t_k) \to 0$ as $k \to \infty$, since $\lim_{k\to\infty} x_1(t_k) = 0$, and for $i \geqq 2$, $x_i'(t_k) = c_i x_i(t_k)$ where $c_i = -D + p_i(S(t_k)) \leqq -D + \max_{0 \leqq S \leqq \bar{\lambda}} p_i(S) < 0$. Since $\lim_{k\to\infty} z'(t_k) = 0$, it follows that $\lim_{k\to\infty} x_i'(t_k) = 0$ and therefore $\lim_{k\to\infty} x_i(t_k) = 0$ for $i \geqq 2$. Thus $\lim_{k\to\infty} x_i(t_k) = 0$ for all $i \in I$, which implies that $\lim_{k\to\infty} S(t_k) = S^0 > \bar{\lambda}$, a contradiction. Theorem 4.6 now follows.

LEMMA 4.7. *Let $(S(t), x_1(t), \cdots, x_n(t))$ be any solution of $(2.1)_{\mathscr{S}}$. Let $\gamma \in \Gamma$. Then there do not exist t_1, t_2 with $0 \leqq t_1 < t_2$, such that*

(i) $S(t_1) = S(t_2) = \gamma > S(t)$, *for $t_1 < t < t_2$*

and

(ii) $S'(t_1) \leqq 0 \leqq S'(t_2)$.

Proof. In this proof we adopt the convention that the result of summation over an empty index set is zero.

Recall that $\Gamma = \{\lambda_i : \lambda_i < S^0\} \cup \{\mu_j : \mu_j < S^0\}$, and that the elements of Γ have been relabelled as $\gamma_1 < \gamma_2 < \cdots < \gamma_k < S^0$. The proof will proceed by induction on the index set $\{1, 2, \cdots, k\}$.

Let $\gamma = \gamma_1 = \lambda_1$, and suppose that (i) and (ii) hold. Since $S(t_1) = \gamma_1 = \lambda_1$, γ_1 is the endpoint of a component of Q, and so it follows from Lemma (4.4) that $S'(t_1) > 0$, contradicting (i). Therefore the lemma holds for $\gamma = \gamma_1$.

Now suppose the lemma is true for $\gamma = \gamma_m$, for all m with $1 \leqq m \leqq h - 1$, where $2 \leqq h \leqq k$. Let $\gamma = \gamma_h$ and suppose that (i) and (ii) are satisfied.

Let $a_i = (p_i(\gamma_h) - D)/y_i$, $i \in I$. Then $x_i'(t_j)/y_i = a_i x_i(t_j)$, $j = 1, 2$; $i \in I$, and so (ii) and (4.4) imply that

$$(4.5) \qquad -\sum_{i=1}^{n} a_i x_i(t_1) \leqq -\sum_{i=1}^{n} a_i x_i(t_2).$$

Suppose that $\gamma_h = \lambda_l$ for some $l \geqq 2$ (note this implies $n \geqq 2$). Define J to be $\{j \in I : \mu_j < \lambda_l\}$ and L to be $\{1, \cdots, l-1\}$. Observe that the a_i have the following signs:

$$(4.6) \qquad \begin{aligned} a_i > 0, &\quad i \in L \backslash J, \\ a_i \leqq 0, &\quad i \in (I \backslash L) \cup J. \end{aligned}$$

with strict inequality except for $i = l$. Rearranging (4.5) gives

$$(4.7) \qquad -\sum_{i \in (I \backslash L) \cup J} a_i (x_i(t_1) - x_i(t_2)) \leqq \sum_{i \in (L \backslash J)} a_i (x_i(t_1) - x_i(t_2)).$$

By (i), $S(t) < \lambda_l$ for $t_1 < t < t_2$. The inductive hypothesis gives $S(t) \geqq \gamma_{h-1}$, i.e. $S(t) \geqq \max(\lambda_{l-1}, \max_{i \in J} \mu_i)$, with (by continuity of $S(t)$) strict inequality in some nonempty

subinterval U of (t_1, t_2). Thus for $t_1 < t < t_2$, we have

$$p_i(S(t)) - D \begin{cases} \geq 0, & i \in L \backslash J, \\ \leq 0, & i \in (I \backslash L) \cup J \end{cases}$$

with strict inequality in U, and so

$$(4.8) \qquad x_i(t_1) - x_i(t_2) \begin{cases} < 0, & i \in L \backslash J, \\ > 0, & i \in (I \backslash L) \cup J. \end{cases}$$

By (4.6) and (4.8), the left-hand side of (4.7) is nonnegative and the right-hand side is nonpositive, which is possible only if all a_i are zero. But only a_l is zero and since $n \geq 2$ in this case, we have a contradiction.

Now suppose that $\gamma_h = \mu_l$ for some l. We define $K = \{i \in I: \mu_i < \mu_l\}$, $M = \{i \in I: \lambda_i > \mu_l\}$, and rearrange (4.5) to give

$$(4.9) \qquad -\sum_{i \in K \cup M} a_i(x_i(t_1) - x_i(t_2)) \leq \sum_{i \in I \backslash (K \cup M)} a_i(x_i(t_1) - x_i(t_2)).$$

A similar argument as before gives a contradiction. Thus the induction is complete, and the lemma is proved.

LEMMA 4.8. *Let* $(S(t), x_1(t), \cdots, x_n(t))$ *be a solution of* $(2.1)_\mathscr{S}$ *and let* γ_l, γ_{l+1} *be consecutive elements of* Γ. *Then, for all sufficiently large* t, *precisely one of the following occurs*:

(a) $S(t) < \gamma_l$, *or*

(b) $\gamma_l \leq S(t) \leq \gamma_{l+1}$, *or*

(c) $S(t) > \gamma_{l+1}$.

Proof. If for all t, $S(t) \notin [\gamma_l, \gamma_{l+1}]$, then clearly (a) or (c) must hold. Suppose then that $\gamma_l \leq S(\tau_0) \leq \gamma_{l+1}$ for some τ_0. If $\gamma_l \leq S(t) \leq \gamma_{l+1}$ for all $t \geq \tau_0$, then (b) holds. If there exists $\bar{\tau}_0 > \tau_0$ such that $S(\bar{\tau}_0) < \gamma_l$, then there will exist τ_1 with $\tau_0 \leq \tau_1 \leq \bar{\tau}_0$, such that $S(\tau_1) = \gamma_l > S(t)$ for $\tau_1 < t < \bar{\tau}_0$, and $S'(\tau_1) \leq 0$. It follows from Lemma 4.7 that we must have $S(t) < \gamma_l$ for all $t > \tau_1$, i.e. (a) holds. If there exist $\bar{\tau}_1 > \tau_0$ such that $S(\bar{\tau}_1) > \gamma_{l+1}$, then either $S(t) > \gamma_{l+1}$ for all $t > \bar{\tau}_1$, in which case (c) holds, or there exists $\tau_2 > \bar{\tau}_1$ such that $S(\tau_2) = \gamma_{l+1}$, and $S'(\tau_2) \leq 0$. By Lemma 4.7 again, we must then have $S(t) < \gamma_{l+1}$ for all $t > \tau_1$. By the preceding argument, we will then have (a) or (b) occurring. This proves the lemma.

LEMMA 4.9. *Let* $(S(t), x_1(t), \cdots, x_n(t))$ *be a solution of* $(2.1)_\mathscr{S}$, *let* (λ_i, μ_j) *be a component of* Q, *and suppose that* $S(t) \in [\lambda_i, \mu_j]$ *for all sufficiently large* t. *Then* $\lim_{t \to \infty} S(t)$ *exists and is equal to* λ_i *or to* μ_j.

Proof. Let $\Gamma_{ij} = \{\lambda_h: \lambda_i \leq \lambda_h \leq \mu_j\} \cup \{\mu_l: \lambda_i \leq \mu_l \leq \mu_j\}$. Since (λ_i, μ_j) is a component of Q, we have $\lambda_i < S^0$, and so Γ_{ij} is a nonempty subset of Γ. With the labelling used for Γ, there exist r, s such that $\lambda_i = \gamma_r < \gamma_{r+1} \leq \gamma_s = \mu_j$. By Lemma 4.8, for each interval $[\gamma_l, \gamma_{l+1}]$, where $r \leq l \leq s - 1$, $S(t)$ is either eventually in that interval or eventually outside it. Since these intervals decompose $[\lambda_i, \mu_j]$, there is some value of l such that $\gamma_l \leq S(t) \leq \gamma_{l+1}$ for all sufficiently large t. If $\gamma_l = \lambda_{\bar{p}}$, say, then $\gamma_{l+1} \leq \mu_{\bar{p}}$ and so $x'_{\bar{p}}(t) \geq 0$ for all sufficiently large t. If $\gamma_l = \mu_q$, say, then it cannot be that $\mu_{\bar{q}} < \mu_q$ for all $\bar{q}$ for which $\lambda_i \leq \lambda_{\bar{q}} < \mu_q$; for otherwise (λ_i, γ_l) is a component of Q, a contradiction since, by assumption, (λ_i, μ_j) is a component of Q, and $\gamma_l < \mu_j$. Thus there exists $\bar{q}$ such that $\lambda_i \leq \lambda_{\bar{q}} < \mu_q = \gamma_l < \gamma_{l+1} \leq \mu_{\bar{q}} \leq \mu_j$, and so $x'_{\bar{q}}(t) \geq 0$ for all sufficiently large t. In either event, therefore, there exists p such that $x'_p(t) \geq 0$ for all sufficiently large t. Since solutions of $(2.1)_\mathscr{S}$ are bounded, $x_p(t)$ converges monotonely to $x_p^* > 0$ as $t \to \infty$. By Lemma 4.2, $\lim_{t \to \infty} S(t) = \gamma$ (where $\gamma = \lambda_p$ or μ_p).

Now we use Lemma 4.3(a) to deduce that $\gamma = \lambda_i$ or μ_j.

The next lemma describes the asymptotic behaviour of the system $(2.1)_{\mathscr{S}}$.

LEMMA 4.10. *Let* $(S(t), x_1(t), \cdots, x_n(t))$ *be a solution of* $(2.1)_{\mathscr{S}}$. *Then* $\lim_{t \to \infty} S(t)$ *exists and is equal to* γ, *where* γ *is either* S^0 *or is the endpoint of a component of* Q. *If* $\gamma = S^0$, *then* $\lim_{t \to \infty} x_j(t) = 0, j \in I$. *If* $\gamma = \lambda_i$ *or* μ_i, *the endpoint of a component of* Q, *then* $\lim_{t \to \infty} x_i(t) = y_i(S^0 - \gamma)$, $\lim_{t \to \infty} x_j(t) = 0, j \neq i$.

Proof. By Lemma 4.5, $S(t)$ is either eventually interior or exterior to the closure of each component of Q. Since Q is the union of its (disjoint) components, either $S(t)$ is eventually in the closure of some component $[\lambda_i, \mu_j]$ or is eventually exterior to $\bar{Q}$. In the first case, Lemma 4.9 gives the result. In the second case, $x_i(t)$ is eventually decreasing for all i. By (4.4), $S(t)$ is eventually increasing and therefore has a limit as $t \to \infty$. Lemma 4.3 now completes the proof.

It is evident that we can replace $(2.1)_{\mathscr{S}}$ in Lemma 4.10 by $(2.1)_{\mathscr{S}_H}$, where H is any subset of I, provided we also replace Q by $Q_H = (\cup_{h \in H} (\lambda_h, \mu_h)) \cap Q$.

5. Proofs of the main results.

We introduce the following notation for the critical points of (2.1):

$$E_{\lambda_k} = (S, x_1, \cdots, x_n): S = \lambda_k; x_k = y_k(S^0 - \lambda_k); x_l = 0, l \neq k, \quad \text{defined for } \lambda_k < S^0,$$

$$E_{\mu_k} = (S, x_1, \cdots, x_n): S = \mu_k; x_k = y_k(S^0 - \mu_k); x_l = 0, l \neq k, \quad \text{defined for } \mu_k < S^0,$$

$$E_{S^0} = (S^0, 0, \cdots, 0).$$

We let $\mathscr{E}$ denote the set of all critical points of (2.1), i.e.

$$\mathscr{E} = \left(\bigcup_{\lambda_k < S^0} \{E_{\lambda_k}\} \right) \cup \left(\bigcup_{\mu_k < S^0} \{E_{\mu_k}\} \right) \cup \{E_{S^0}\}.$$

We will also consider the following subsets of $\mathscr{E}$:

$$L = \{E_{\lambda_k}: \lambda_k \text{ is a left endpoint of a component of } Q\}.$$

$$R = \{E_{\mu_k}: \mu_k \text{ is a right endpoint of a component of } Q\}.$$

$$\mathscr{E}^* = \begin{cases} \mathscr{E} \setminus (L \cup R \cup \{E_{S^0}\}) & \text{if } S^0 \notin Q, \\ \mathscr{E} \setminus (L \cup R) & \text{if } S^0 \in Q. \end{cases}$$

In order to prove Theorems 3.3 and 3.4 we first establish the local stability of the critical points of (2.1). Since this is obtained fairly routinely from standard linearization procedures, we summarize this result, without proof, in the following lemma.

LEMMA 5.1. *All the points in* $\mathscr{E}$ *are hyperbolic critical points* (i.e. *all the associated eigenvalues of the linearized system have nonzero real parts*). *Furthermore,*

(i) *For the system* (2.1), *the critical points in* L *are all asymptotically stable.*

(ii) *The critical points in* R *are all unstable, but each has an n-dimensional stable manifold.*

(iii) *The critical point* $(S^0, 0, \cdots, 0)$ *is asymptotically stable iff* $S^0 \notin Q$. (*Note that* $S^0 \in \partial Q$ *is excluded by the generic condition* (2.7).)

(iv) *The critical points in the set* $\mathscr{E}^*$ *are all unstable. The stable manifold of each of these points is entirely contained in the boundary of* $\mathbb{R}^{n+1}_+$ (*which we identify with* $(S, x_1, \cdots, x_n)$-*space*).

The following lemma will be useful. It can be obtained either by the use of Hartman's linearization theorem [12] or by the method of isolating blocks [8], and a proof may be found in Appendix 1 of a paper of Freedman and Waltman [10].

LEMMA 5.2. *Let* P *be an isolated hyperbolic critical point in the omega-limit set* $\Omega(X)$ *of an orbit through* X *of a dynamical system. Then either* $\Omega(X) = \{P\}$, *or there*

exist points P^s and P^u in $\Omega(X)$, with $P^s \in W^s(P)\backslash\{P\}$ and $P^u \in W^u(P)\backslash\{P\}$, where $W^s(P)$ and $W^u(P)$ denote the stable and unstable manifold of P respectively.

LEMMA 5.3. (i) *No point of the set $\mathscr{E}^*$ is in the omega-limit set of any solution of* (2.1).

(ii) *If a point of the set $\mathscr{E}\backslash\mathscr{E}^*$ is in the omega-limit set of some solution of* (2.1), *then it is the only point in the omega-limit set of that solution.*

Proof. Let $(S(t), x_1(t), \cdots, x_n(t))$ be a solution of (2.1) and let Ω be its omega-limit set. Suppose that $P \in \Omega \cap \mathscr{E}^*$. Then P is of the form E_{λ_l}, E_{μ_l} or E_{S^0}, and $\mathscr{I} = \{i \in I: \lambda_i < \lambda_l < \mu_i\}$ (resp. $\{i \in I: \lambda_i < \mu_l < \mu_i\}$, $\{i \in I: \lambda_i < S^0 < \mu_i\}$) is nonempty. By Lemma 5.1, $W^s(P) \subset \partial\mathbb{R}_+^{n+1}$. Since the trajectory of $(S(t), x_1(t), \cdots, x_n(t))$ is contained in int R_+^{n+1}, Lemma 5.2 yields the existence of a point $P^u \in (W^u(P)\backslash\{P\}) \cap \Omega$ and we may assume that P^u and the negative semi-orbit through P^u are as close to P as we wish. Let this negative semi-orbit be denoted $(\bar{S}(t), \bar{x}_1(t), \cdots, \bar{x}_n(t))$, $t \le 0$, so that $P^u = (\bar{S}(0), \bar{x}_1(0), \cdots, \bar{x}_n(0))$. Define $\mathscr{J}$ to be $\{j \in I: \bar{x}_j(0) \ne 0\}$.

If $j \notin \mathscr{J} \cup \{l\}$ (if $j \notin \mathscr{J}$ in the case that $P = E_{S^0}$), then $p_j(\bar{S}(t)) - D < 0$ for $t \le 0$ and so $\bar{x}_j(t)$ is nonincreasing on $(-\infty, 0]$. Since $\bar{x}_j(t) \to 0$ as $t \to -\infty$, it follows that $\bar{x}_j(t) \equiv 0$ on $(-\infty, 0]$ and so $\bar{x}_j(0) = 0$.

On the other hand, there must exist some $j \in \mathscr{J}$ with $\bar{x}_j(0) > 0$, otherwise P^u would belong to $W^s(P)$. Hence the trajectory of the solution $(\bar{S}(t), \bar{x}_1(t), \cdots, \bar{x}_n(t))$ is in the relative interior of the subsimplex $\mathscr{S}_{\mathscr{J}}$ of $\mathscr{S}$. Since $(\lambda_j, \mu_j) \cap (\lambda_k, \mu_l) \ne \varnothing$ for all $j \in \mathscr{J}$ ($S^0 \in (\lambda_j, \mu_j)$ for all $j \in \mathscr{J}$ in the case that $P = E_{S^0}$), it follows that $Q_{\mathscr{J}}$ is connected, say $Q_{\mathscr{J}} = (\lambda_m, \mu_M)$. By Lemma 4.10 applied to $(2.1)_{\mathscr{S}_{\mathscr{J}}}$, we have

$$(5.1) \qquad\qquad \bar{S}(t) \to \lambda_m, \mu_M \text{ or } S^0.$$

(a) Suppose that $P = E_{\lambda_l}$.

We may assume that P^u is so close to P that $\bar{S}(t) \in (\lambda_j, \mu_j)$ for all $t \le 0$, for all $j \in \mathscr{J}\backslash\{l\}$. We cannot have $\bar{S}(t) > \lambda_l$ for any $t \in (-\infty, 0]$, for otherwise there exists $\tau \in (-\infty, 0]$ with $\bar{S}'(\tau) > 0$ and $\bar{S}(\tau) \in (\lambda_j, \mu_j)$ for all $j \in \mathscr{J}$, which implies that $\bar{x}_j'(\tau) > 0$, contradicting $\bar{S}' + \sum_{j \in \mathscr{J}} \bar{x}_j'/y_j \equiv 0$. Thus $\bar{S}(t) < \lambda_l$ for all t. Since $\lambda_m < \lambda_l < \mu_M$ (and $S^0 > \lambda_l$), we must have $\bar{S}(t) \to \lambda_m$ as $t \to \infty$. By Lemma 4.10 it follows that $E_{\lambda_m} \in \Omega$.

Repeating this argument inductively, we may eventually conclude that $E_{\lambda_i} \in \Omega$, where $E_{\lambda_i} \in L$. By Lemma 5.1, E_{λ_i} is asymptotically stable for (2.1), so $\Omega = \{E_{\lambda_i}\}$, contradicting $E_{\lambda_l} \in \Omega$.

(b) Suppose that $P = E_{S^0}$.

By arguments similar to the above, we find that $E_{\lambda_m} \in \Omega$, and obtain a contradiction.

(c) Suppose that $P = E_{\mu_l}$.

An argument similar to that used in (a) shows that $\bar{S}(t) > \mu_l$ for all t and then (5.1) implies that $\lim_{t \to \infty} \bar{S}(t) = \mu_M$ or S^0. Repeating this argument inductively, we arrive at the conclusion that either $E_{\mu_j} \in \Omega$ where $E_{\mu_j} \in R$ or $E_{S^0} \in \Omega$. Suppose that $E_{S^0} \in \Omega$. If $E_{S^0} \in \mathscr{E}^*$, we are back in case (b) and obtain a contradiction. If $E_{S^0} \notin \mathscr{E}^*$, it is asymptotically stable for (2.1), by Lemma 5.1, so that $\Omega = \{E_{S^0}\}$, contradicting $E_{\mu_l} \in \Omega$.

Suppose that $E_{\mu_j} \in \Omega$, but $\Omega \ne \{E_{\mu_j}\}$. Then $(W^u(E_{\mu_j})\backslash\{E_{\mu_j}\}) \cap \Omega \ne \varnothing$, by Lemma 5.2. By considering the subsimplex $\mathscr{S}_{\{j\}}$, we find that either E_{λ_j} or $E_{S^0} \in \Omega$, and obtain a contradiction by the preceding arguments.

This proves the first assertion of the lemma. If $P \in \Omega$ and $P \in L$, or $P = E_{S^0}$ in the case that $S^0 \notin \bar{Q}$, then P is asymptotically stable and so $\Omega = \{P\}$. If $P \in R$, then $\Omega = \{P\}$. Otherwise we obtain a contradiction as in case (c) discussed above. This proves the second part of the lemma.

Proof of Theorem 3.3. Since $\mathscr{S}$ is globally attracting for (2.1), the omega-limit set Ω, of any solution of (2.1) is a union of trajectories lying entirely in $\mathscr{S}$, where each

such trajectory is a solution of $(2.1)_{\mathscr{S}_H}$ for some $H \subset I$. By the remark following Lemma 4.10, applied to $(2.1)_{\mathscr{S}_H}$ for any $H \subset I$, every solution of $(2.1)_{\mathscr{S}_H}$ converges to a point in $\mathscr{E}$. Since the omega-limit set is closed, Ω must contain a point of $\mathscr{E}$. The result follows by Lemma 5.3.

Proof of Theorem 3.4. Immediate from Theorem 3.3 and Lemma 5.1.

Corollary 3.5 follows at once from Theorem 3.4.

Theorem 3.6 can be proved using arguments similar to those used to prove Theorem 3.4.

6. Discussion. We have considered a model of purely exploitative competition between n populations in a chemostat for a single essential nonreproducing growth-limiting substrate, which may be inhibiting at high concentrations. Our results predict that at most one of the competing populations survives, i.e. there is competitive exclusion. However, the outcome may be initial condition dependent. The global dynamics of the model are in a sense, trivial, in that all solutions have limiting asymptotic behaviour. There are a finite number of locally asymptotically stable equilibria whose domains of attraction partition the (strictly) positive $(S, x_1, x_2, \cdots, x_n)$ cone, their boundaries being comprised of the stable manifolds of some of the unstable equilibria of the system (if all the λ_i and μ_i are finite, there are at most $2n + 1$ equilibria, at most $n + 1$ of which are asymptotically stable). These results are not surprising. According to Fredrickson [9], there is much experimental evidence that "pure and simple competitors will not coexist indefinitely in a system that is spatially homogeneous and that is subject to time-invariant external influences", which is precisely the case in the biological system we consider.

On the attracting simplex $\mathscr{S}$, we could eliminate S from the model to obtain a system of interaction between the x_i. However, the nonmonotone nature of the functions p_i does not allow this system to satisfy the hypotheses of the competition models studied by Armstrong and McGehee [3] or by Hirsch [14]. Our results also contrast with the example given by Nitecki [22] of competition for a single resource, where competitive exclusion does not hold, and the examples of competition for a single reproducing resource (prey) in which coexistence occurs for a variety of models with monotone uptake (predation) responses [6], [7], [18], [19], [26].

Provided that conditions (2.6) and (2.7) hold, our results are easily extended to models with uptake functions p_i that have an arbitrary number of "break-even" concentrations, instead of the two, (λ_i, μ_i) considered in this paper. If these genericity assumptions are not made, more delicate, but technical, arguments are needed.

We have used the same wash-out rate D for both substrate and microorganism populations. This is equivalent to assuming that the death rates of the microorganism populations are negligible compared with the wash-out rate. It would be interesting to see if similar results hold for different wash-out rates (or death rates), D_i. Hsu [15] has carried out the analysis for this situation in the case of Michaelis–Menten kinetics.

To illustrate our results, we consider the following (at least, theoretical) application to water purification. Here we are motivated by experimental work of Yang and Humphrey [30]. Suppose that there is one contaminant, say phenol, in the water supply, and that S^0, the input concentration of phenol, is high. Suppose also that certain microorganisms feed on phenol in such a way that it is growth-limiting at low concentrations, but inhibits growth at high concentration (e.g. Pseudomonas putida and Trichosporon cutaneum). Let A denote an acceptable concentration of phenol in the water supply and assume $A \ll S^0$. Suppose that microorganism 1 is harmless and that $\lambda_1 < A$ but $\mu_1 \ll S^0$. If the initial concentration of phenol in the water supply is relatively high,

and microorganism 1 is used alone in an attempt to reduce the phenol level, then it is likely to wash out of the system and the concentration of phenol would approach the unacceptable level S^0. On the other hand, suppose that microorganism n has $A < \lambda_n < S^0 < \mu_n$. If microorganism n is used alone, $S(t)$ would approach the value λ_n, which is again unacceptable. However, if we could find microorganisms $2, \cdots, n-1$, so that (λ, μ) intervals overlap in such a way as to form a single component of Q, containing S^0, then we would have $\lim_{t \to \infty} S(t) = \lambda_1 < A$, $\lim_{t \to \infty} x_1(t) = y_1(S^0 - \lambda_1)$ and $\lim_{t \to \infty} x_j(t) = 0, j > 1$, arriving eventually at a tolerable situation.

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