

PREDATOR - MEDIATED COEXISTENCE IN A CHEMOSTAT: COEXISTENCE AND COMPETITION REVERSAL

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Abstract. If a system of several populations of microorganisms compete exploitatively for a single nonreproducing limiting nutrient which is introduced into and washed out of the system at a constant rate, then competitive exclusion results. Provided that there are no inhibition effects, the population requiring the lowest "break-even" concentration of nutrient will be the winner. This outcome can be changed if a predator population is introduced into the system. In this paper we explore some of the possibilities of coexistence and competition reversal that may arise.

Keywords: Chemostat; coexistence; predator influence; competition reversal

INTRODUCTION

If two or more distinct populations of microorganisms compete for a non-reproducing, limiting substrate, then in the simpler circumstances, sometimes referred to as "pure competition" it would appear that at most one of the populations can be maintained. There is a useful laboratory experiment that models this type of competition, namely the chemostat, in which the competing populations are sustained in a growth chamber and a single essential, growth-limiting nutrient is supplied at a constant rate from a feed bottle. Removal of nutrient, microorganisms, by-products and other growth media also takes place, usually at the same rate at which nutrient is supplied so that the volume of the system is preserved. The chemostat can be regarded as a rather successful, if somewhat simplified, aid to the understanding of growth and competition kinetics in a natural environment, in that individual features which affect the outcomes (rates of nutrient input and washout, "Michaelis-Menten constants", inhibition factors, etc.) are under the control of the experimenter. For a detailed account of some of the experimental features of the chemostat, see, for example (Aris & Humphrey, 1977; Hansen & Hubbell, 1981; Jost et al., 1973; Monos, 1942; Novick & Szilard, 1950; Veldamp, 1977; Waltman et al., 1980).

The chemostat is of interest too, to the modeller of competitive systems since it provides a simple prototype on which to test modelling hypotheses.

Under the assumption that the chemostat can be described by a system of ordinary differential equations in which Michaelis-Menten kinetics pertain, Hsu et al. (1977) gave a complete mathematical analysis. They showed that the competitor requiring the lowest "break-even" concentration of nutrient will be the only population to survive. By "break-even" concentration we mean the level of nutrient required to compensate for the natural death (washout) rate of the population so that it could be maintained in the absence of competition. This result was extended to the case of arbitrary monotone nutrient uptake rates by Armstrong & McGehee (1980). We gave an essentially complete analysis of the model with arbitrary nutrient uptake rates - without the assumption of monotonicity (Butler & Wolkowicz, 1985). This allows one to consider the situation, for example, in which inhibition effects occur. The

outcome is still that at most one population will survive, though now that survivor may depend on the initial configuration of the system.

There are a number of ways in which we might modify the chemostat to alter the outcome of the competition as described above. One way is to supply the nutrient at a periodic rate rather than at a constant rate, or to allow washout to take place at a periodic rate (Butler et al., 1985; Smith, 1981). Another possibility is to allow interspecies interference. A third possibility, which is the one we wish to pursue in this paper, is to introduce into the system a population which predate on one of the competing microorganisms. The authors first considered a model for that situation in (Butler & Wolkowicz, 1986), leading to a system of four populations (substrate, two competitors and predator), and we shall summarize some of our results later.

The purpose of this present paper is to initiate an explanation of what can happen if a predator is introduced into a system with three or more competing microorganisms. Although our results are far from complete at this point, we have been able to discover, both numerically and qualitatively, some unexpected consequences which could not have easily been predicted from our earlier studies with two competitors.

MODEL EQUATIONS

Let $S(t)$ denote the concentration of nutrient at time t , $x_i(t)$ the concentration of the i th microorganism population for $i = 1, 2, \dots, n$, and $y(t)$ the concentration of the predator population. In the most general model to be considered, we allow the predator to predate upon the j th competing population, and obtain a system of ordinary differential equations

$$\begin{aligned} S'(t) &= 1 - S(t) - \sum_{i=1}^n x_i(t)p_i(S(t)) \\ x_i'(t) &= x_i(t)\{-1 + p_i(S(t))\}, \\ &\quad i = 1, 2, \dots, n; i \neq j \quad (1) \\ x_j'(t) &= x_j(t)\{-1 + p_j(S(t))\} - y(t)q_j(x_j(t)) \\ y'(t) &= y(t)\{-1 + q_j(x_j(t))\} \end{aligned}$$

The nutrient uptake functions $p_i(S)$ are assumed to be monotone increasing with S , such that $p_i(0) = 0$ and such that there exists a unique positive number λ_i for which $p_i(\lambda_i) = 1$. λ_i is then the "break-even" concentration required for population x_i to be maintained in the absence of competition or predation, and we assume that our competing population have been labelled so that $0 < \lambda_1 < \lambda_2 < \dots < \lambda_n < 1$. The predation function q_j is also assumed to be monotone increasing with $q_j(0) = 0$, and we assume that there exists a unique positive number δ_j for which $q_j(\delta_j) = 1$. Later on we shall introduce an additional parameter to describe the predation function. We have assumed that each $\lambda_i < 1$ otherwise the i th competitor will always wash out of the system, regardless of the competition. In (1), input and washout rates have been normalized to be 1. Finally, for technical mathematical reasons, we assume that the p_i and q_j are continuously differentiable functions and that $p_i'(\lambda_i) > 0$, $q_j'(\delta_j) > 0$.

PREDATION ON A LESS-FAVoured COMPETITOR

In the absence of any predation, x_1 is the favoured competitor (with the lowest λ value); x_2, \dots, x_n will all wash out of the system and x_1 will be maintained asymptotically in an equilibrium state. Not surprisingly, if the predator predate on a competitor other than x_1 , the competitive outcome will be unchanged. This is our first result and subsequently we need only consider the system (1) with $j = 1$.

Theorem 1 Let $j \geq 2$. Then for any solution of (1) with positive initial conditions, we shall have $\lim_{t \rightarrow \infty} S(t) = \lambda_1$, $\lim_{t \rightarrow \infty} x_1(t) = 1 - \lambda_1$, $\lim_{t \rightarrow \infty} x_k(t) = 0$, $k = 2, \dots, n$, and $\lim_{t \rightarrow \infty} y(t) = 0$.

PREDATION ON THE FAVoured COMPETITOR IN A MODEL WITH TWO COMPETITORS

(1) with $j = 1$, $n = 2$ was considered by Butler & Wolkowicz (1986). To discuss the result from that paper which concerns us here, it will be necessary to introduce a positive parameter δ into the predation function $q = q_1$, and write the system as

$$\begin{aligned} S'(t) &= 1 - S(t) - \sum_{i=1}^2 x_i(t)p_i(S(t)) \\ x_1'(t) &= x_1(t)\{-1 + p_1(S(t))\} - y(t)q(\delta, x_1(t)) \\ x_2'(t) &= x_2(t)\{-1 + p_2(S(t))\} \\ y'(t) &= y(t)\{-1 + q(\delta, x_1(t))\} \end{aligned} \quad (2)$$

We assume that $q(\delta, \delta) = 1$ and that $\lim_{\delta \rightarrow 0^+} q(\delta, \epsilon) = \infty$ for any fixed $\epsilon > 0$. For example, if q represents Lotka-Volterra, Michaelis-Menten or multiple saturation kinetics, then q can be parametrized in this way. We can regard decreasing the parameter δ as corresponding to increasing the intensity of predation.

Before stating the following result, it will be appropriate to give a precise definition of what we mean by persistence of the system (2)

Definition. (2) will be called persistent if for all solutions with positive initial conditions, we have each solution component bounded away from zero as time gets large, i.e. $\lim_{t \rightarrow \infty} z(t) > 0$, where z stands for S , x_1, x_2 or y .

In other words, the system is persistent if all populations coexist in the system, regardless of initial conditions.

Theorem 2 (Butler & Wolkowicz, 1986). If δ is sufficiently small, i.e. the intensity of predation is sufficiently high then (2) is persistent.

Theorem 2 asserts that x_2 can compete successfully with x_1 provided the predation is sufficiently intense. The coexistence of the two competitors may not necessarily be in equilibrium; some examples indicate that the populations undergo periodic oscillations.

PREDATION ON THE FAVoured COMPETITOR IN A MODEL WITH THREE COMPETITORS

We consider (1), with $j = 1$, $n = 3$. As in below, it will be convenient to introduce a parameter into the predation function $q = q_1$, and write (1), as

$$\begin{aligned} S'(t) &= 1 - S(t) - \sum_{i=1}^3 x_i(t)p_i(S(t)) \\ x_1'(t) &= x_1(t)\{-1 + p_1(S(t))\} - y(t)q(\delta, x_1(t)) \\ x_i'(t) &= x_i(t)\{-1 + p_i(S(t))\}, \quad i = 2, 3 \\ y'(t) &= y(t)\{-1 + q(\delta, x_1(t))\} \end{aligned} \quad (3)$$

We recall that in pure competition, x_2 outcompetes x_3 , and in the absence of predation, x_1 outcompetes both of them. Based

on our knowledge of the behaviour of (2), we might conjecture that at a certain intensity of predation, x_2 can coexist with x_1 , and either (a) x_3 is unable to compete successfully at any level of predation or (b) if the intensity of predation is sufficiently high, x_3 can coexist with x_1 and x_2 .

Possibility (a) does occur if the kinetics of the system take a certain form; indeed we can make such a statement about a model with n competitors:

Theorem 3. Consider the system

$$\begin{aligned}
 S'(t) &= 1 - S(t) - \sum_{i=1}^n x_i(t)p_i(S(t)) \\
 x_1'(t) &= x_1(t)\{-1 + p_1(S(t))\} - y(t)q(\delta, x, (t)) \\
 x_i'(t) &= x_i(t)\{-1 + p_i(S(t))\}, \quad i = 2, 3, \dots, n \\
 y'(t) &= y(t)\{-1 + q(\delta, x_1(t))\} \quad (4)
 \end{aligned}$$

Suppose the predation function q is of Lotka-Volterra type and the predation functions p_i are either of Lotka-Volterra type or of Michaelis-Menten type. Then for all $\delta > 0$, we will have $\lim_{t \rightarrow \infty} x_i(t) = 0$ for $i \geq 3$ and the system will reduce asymptotically to (2).

As yet we have not managed to demonstrate either theoretically or numerically that possibility (b) - coexistence of all three competitors - can take place.

What we have discovered is the rather surprising result that a third possibility can occur, that of the reversal of competitive outcome between x_2 and x_3 .

Theorem 4. In (3), let the kinetics of each interaction be Michaelis-Menten. Specifically, let

$$q(\delta, x) = \frac{mx}{\delta(m-1) + x}, \quad p_i(S) = \frac{m_i S}{a_i + S} \quad (i=1, 2, 3),$$

where m, m_i, a_i are positive constants.

Then there is a choice of parameter values δ, m, m_i, a_i such that $0 < \lambda_1 < \lambda_2 < \lambda_3 < 1$ and for which the following is true:

(i) for all solutions of (3) with positive initial conditions, with the exception of those solutions that lie on a single exceptional orbit,

we have $\lim_{t \rightarrow \infty} x_1(t) > 0, \lim_{t \rightarrow \infty} x_3(t) > 0$.

(ii) for at least some of the solutions of (3) with positive initial conditions, we have

$$\lim_{t \rightarrow \infty} x_2(t) = 0.$$

SKETCH OF PROOFS

Some general remarks are in order:

1. Under our hypotheses, the uptake and predation functions are sufficiently smooth that initial value problems for (1) and subsequent specializations of this system are uniquely solvable.

2. Solutions with positive (non-negative) initial conditions remain positive (non-negative) and exist and are bounded for all positive time. Indeed the hyperplane $\Pi: S + \sum_{i=1}^n x_i + y = 1$ is a global attractor for solutions with positive initial conditions.

Proof of Theorem 1. By virtue of the above remarks, any solution $(S(t), x_1(t), \dots, x_n(t), y(t))$ of (1) with positive initial conditions has a nonempty, compact omega limit set Ω lying in Π , and Ω consists of full orbits in Π . Let $(\bar{S}, \bar{x}_1, \dots, \bar{x}_n, \bar{y})$ be an orbit in Ω , and denote $\bar{S}(t) + \sum_{i=1}^n \bar{x}_i(t) + \bar{y}(t)$ by $\bar{z}(t)$. Then $\bar{z}(t) \equiv 1$, and so $\bar{z}'(t) \equiv 0$. Suppose that there exists t_0 such that

$$\bar{S}(t_0) = \lambda_1, \quad \bar{S}'(t_0) \leq 0.$$

Then

$$\begin{aligned}
 0 &= \bar{z}'(t_0) = \bar{S}'(t_0) + \sum_{i=1}^n \bar{x}_i'(t_0) + \bar{y}'(t_0) \\
 &\leq \sum_{i=1}^n \bar{x}_i(t_0)\{-1 + p_i(\lambda_1)\} - \bar{y}(t_0) \\
 &< 0,
 \end{aligned}$$

which is a contradiction. Thus there is no such t_0 . This leaves the following possibilities:

- (i) $\bar{S}(t) \leq \lambda_1$ for all t , in which case $\lim_{t \rightarrow \infty} \bar{x}_i(t) = 0$ for all $i \geq 2$.
- (ii) $\bar{S}(t_1) > \lambda_1$ for some t_1 , in which case $\bar{S}(t) > \lambda_1$ for all $t \geq t_1$. This implies that $\bar{x}_1(t)$ is monotone increasing for $t \geq t_1$. This in turn implies that $\lim_{t \rightarrow \infty} \bar{S}(t) = \lambda_1$ (see Butler

and Wolkowicz, 1985) and now we must have $\lim_{t \rightarrow \infty} \bar{x}_i(t) = 0$ for all $i \geq 2$. Thus the critical point E_{λ_1} , defined by $S = \lambda_1, x_1 = 1 - \lambda_1, x_2 = \dots = x_n = y = 0$, belongs to Ω . But it is easily verified that E_{λ_1} is asymptotically stable, and so we have $\Omega = \{E_{\lambda_1}\}$, which implies that the given solution of (1) satisfies $\lim_{t \rightarrow \infty} S(t) = \lambda_1, \lim_{t \rightarrow \infty} x_1(t) = 1 - \lambda_1, \lim_{t \rightarrow \infty} x_2(t) = \dots = \lim_{t \rightarrow \infty} x_n(t) = \lim_{t \rightarrow \infty} y(t) = 0$, as claimed.

Proof of Theorem 3. This is proved for general n with the use of a Liapunov function in much the same way that the same result is proved in the special case $n = 2$ (i.e. for the system (2)) by Wolkowicz (1984). We omit the computational details.

Proof of Theorem 4. Denote the non-negative cone in (S, x_1, x_2, x_3, y) -space by C . Fix a_1, a_2, a_3, m_1, m_2 , so that $a_2 < a_3; m_1, m_2 > 1$ and $\lambda_1 < \lambda_2$. (For uptake functions $p_i(S)$ of the form assumed in this theorem, $\lambda_i = a_i / (m_i - 1)$). There is an interval of values of $m_3 \geq m_2$ for which we shall have $\lambda_2 < \lambda_3$. If $\delta > 0$ is chosen sufficiently small, the system (3) will have the following features:

(i) the critical points are the following seven points in C :

$$E_1 = (1, 0, 0, 0, 0), E_{\lambda_1} = (\lambda_1, 1 - \lambda_1, 0, 0, 0),$$

$$E_{\lambda_2} = (\lambda_2, 0, 1 - \lambda_2, 0, 0),$$

$$E_{\lambda_3} = (\lambda_3, 0, 0, 1 - \lambda_3, 0), E_s^* = (S^*, \delta, 0, 0, y^*),$$

where

$$y^* = \delta(-1 + p_1(S^*)), 1 - S^* = \delta p_1(S^*),$$

$$\hat{E}_{\lambda_2} = (\lambda_2, \delta, \hat{x}_2, 0, \hat{y}_2), \hat{E}_{\lambda_3} = (\lambda_3, \delta, 0, \hat{x}_3, \hat{y}_3),$$

where

$$\hat{x}_i = 1 - \lambda_i - \delta p_1(\lambda_i), \hat{y}_i = \delta(-1 + p_1(\lambda_i)).$$

(i = 2, 3).

(ii) in the restriction of (3) to the hyperplane $P_2: x_3 = 0, \hat{E}_{\lambda_2}$ is unstable and the restricted system is persistent in (S, x_1, x_2, y) -space with an attractor A_2 which is global except for the critical point \hat{E}_{λ_2} ,

(iii) in the restriction of (3) to the hyperplane $P_3: x_2 = 0, \hat{E}_{\lambda_3}$ is unstable and the restricted system is persistent in (S, x_1, x_3, y) -space with an attractor A_3 which is global except for the critical point \hat{E}_{λ_3} .

(iv) the stable manifold of \hat{E}_{λ_2} intersects the interior of the non-negative cone in (S, x_1, x_2, x_3, y) -space in a single orbit which "connects" \hat{E}_{λ_3} to \hat{E}_{λ_2} .

Next it may be shown that if m_3 is chosen so that λ_3 is close to λ_2 , then the orbits in A_2 uniformly repel in the direction of increasing x_3 , and the orbits in A_3 "uniformly attract" in the direction of decreasing x_2 . Furthermore it may be shown that the collection \mathcal{C} of the invariant sets comprising all the equilibria of the system, together with A_2 and A_3 , form an "acyclic covering" of the omega limit sets of the restriction of (3) to ∂C , i.e. the "boundary flow" defined by (3) is "acyclic" (Butler & Waltman, 1986). Now the stable sets of each of those elements of \mathcal{C} which lie in the plane P_2 are disjoint from the interior of C , with the exception of the singular orbit described in (iv) above. It follows from arguments somewhat similar to those given in Butler & Waltman (1986) that for all solutions of (3) with positive initial conditions, with the exception of those lying on the singular orbit, we have $\lim_{t \rightarrow \infty} x_3(t) > 0$. Now by (iii) and the choice of m_3 , the set A_3 is (locally) asymptotically stable for (3) and so there will exist solutions of (3) for which $\lim_{t \rightarrow \infty} x_2(t) = 0$.

Remarks. 1. The above statements about the local dynamical behaviour near the critical points of the system (3) are a straightforward matter of verification; however, the assertion of the existence of a global manifold which is both the stable manifold of \hat{E}_{λ_2} and the unstable manifold of \hat{E}_{λ_3} , and the discussion concerning the uniform repulsion and attraction of orbits in A_2, A_3 , respectively, require considerably more delicate arguments. The details of this analysis will appear elsewhere.

2. It is evident that the situation can arise in which the outcome between competitors x_2 and x_3 is initial condition dependent. That is to say, the domain of positive initial conditions is split into two nonempty regions,

one of which corresponds to solutions of (3) in which x_2 survives and x_3 dies out, the other which corresponds to the reverse consequence. This may occur if there are locally stable periodic orbits in each of the hyperplanes P_2 , P_3 .

DISCUSSION

For a chemostat with monotone uptake functions in which there is "pure" competition (competition through exploitation of the single, limiting, non-reproducing resource, without predation), one competitor out-competes all of his rivals. There is some belief in ecological circles (Levin, 1970; Paine, 1966) that predation can account for diversity in ecosystems, with the corollary that elimination of the predator may interfere with the balance between competing populations and lead to the collapse of the system or some part of it. Ideally, our long-term goal would be to establish (or refute) the existence of a mechanism of population interactions that supports such a belief. Although we are very far from succeeding in this objective in the current paper, which can only be regarded as a preliminary report on these ideas, we hope that it will cast some light on the possible types of behaviour of these somewhat complex systems.

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