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Microbial Dynamics in a Chemostat:
Competition, Growth, Implications of Enrichment

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1   INTRODUCTION

First, the global dynamics of a basic model of the chemostat in which n populations of microorganisms compete exploitatively for a single, essential, nonreproducing, growth-limiting nutrient, supplied at a constant input rate is discussed. What is known in the case that the species specific death rates are assumed to be negligible compared to the dilution rate, is summarized. Then, an open problem in the case that these death rates are not necessarily insignificant is described.

Next, the differences in the predictions of different models of population growth with regard to the effect of enrichment of the environment are investigated. A problem with the classical model proposed by Verhulst (1838) and with the generalized Gause type models for population growth, with regard to such predictions, is pointed out. Then the predictions of two other models of population growth, each based in a chemostat are considered. The first chemostat model is simply the case $n = 1$ of the competition model already described, that is the case of growth of a single population on a single nutrient that is considered to be limiting. In the second chemostat model, it is assumed that there are two noninhibitory, perfectly substitutable resources that are limiting. Our results show that under certain conditions, the two models make very different predictions

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concerning the outcome of population growth under enrichment by increasing the input concentration of one of the resources, making a case that when a model is to be valid over a range of the operating parameters, predictions of models assuming single resource limitation could be misleading. These results seem to have important implications for the use of models in resource management.

2   THE n-SPECIES COMPETITION MODEL

In this section we consider the following model of microbial competition in a chemostat.

$$
\begin{aligned}
S'(t) &= (S^o - S(t))D - \sum_{i=1}^{n} \frac{x_i(t)p_i(S(t))}{y_i}, \\
\\
x_i'(t) &= x_i(t)\left(-D_i + p_i(S(t))\right), \ i = 1, ..., n,
\end{aligned}
\tag{2.1}
$$

where $S(0) \geq 0$, $x_i(0) > 0$, $i = 1, ..., n$ and S^o, D, D_i, and y_i are positive constants.

In these equations, as in Wolkowicz and Lu (1992), it is assumed for convenience that the volume of the culture vessel is one cubic unit. The culture vessel is also assumed to be well-stirred, so that spatial variation need not be considered and nutrients, microorganisms and byproducts are removed in proportion to their concentrations. $S(t)$ denotes the concentration of the substrate at time t; $x_i(t)$ denotes the concentration of the ith population of microorganisms at time t; S^o denotes the concentration of substrate in the feed bottle. All other nutrients are assumed to be supplied at such quantities that this is the only nutrient that limits growth. $p_i(S(t))/y_i$ denotes the uptake rate of substrate of the ith population. We assume that $p_i(S)$ represents the per-capita growth rate of the ith population so that y_i is a growth yield constant. D denotes the input rate from the feed bottle containing the substrate and the washout rate of substrate, microorganisms, and byproducts from the growth chamber and so constant volume is maintained. Each $D_i = D + \epsilon_i$, where $\epsilon_i > 0$ can be interpreted as the species specific death rate of species x_i. The analysis of the model requires only that $D_i > 0$ and so $\epsilon_i \leq 0$ is also allowed. This leaves the D_i open to other interpretations.

For general background on model (2.1), in the case of both monotone and non-monotone response functions, the reader is referred to Wolkowicz and Lu (1992) and the references given therein. Keeping in mind that certain substrates are growth-limiting when their concentrations are low, as well as growth-inhibiting when their concentrations are sufficiently high, whereas other substrates only limit growth when their concentrations are low, we make the same assumptions as in Butler and Wolkowicz (1985) and Wolkowicz and Lu (1992) on the form of the response functions $p_i, \ i = 1, 2, ..., n$ in model (2.1):

$$
p_i : \mathbf{R}_+ \to \mathbf{R}_+,
\tag{2.2}
$$

$$
p_i \quad \text{is continuously differentiable,}
\tag{2.3}
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p_i(0) = 0,
\tag{2.4}
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and there exist uniquely defined, positive, extended real numbers, called break-even concentrations, λ_i and μ_i, with $\lambda_i \leq \mu_i$, such that

$$p_i(S) < D_i \quad \text{if} \quad S \in (\lambda_i, \mu_i),$$
$$p_i(S) > D_i \quad \text{if} \quad S \notin [\lambda_i, \mu_i].$$

If $p_i(S) < D_i$ for all $S > 0$, then $\lambda_i = \mu_i = +\infty$. On the other hand, if $p_i(S)$ is monotone increasing or if $p_i(S) > D_i$ for all $S > \lambda_i$, then $\mu_i = +\infty$.

Assume that the populations are labelled so that

$$\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n. \tag{2.5}$$

Three prototypes of monotone response functions are:

1. Holling type I: $p_i(S) = r_i S;$

2. Holling type II: $p_i(S) = \frac{c_i S}{a_i + S};$

3. Holling type III: $p_i(S) = \frac{m_i D_i S^2}{(a_i + S)(b_i + S)};$

A prototype for a nonmonotone response function is:

4. inhibition: $p_i(S) = \frac{m_i D_i S}{(a_i + S)(b_i + S)}.$

Forms (1)–(3) are also referred to as Lotka-Volterra, Michaelis-Menten, and sigmoidal response functions, respectively. For a derivation of the model in the special case that the response functions are Holling type II, the reader is referred to Waltman, Hubbell, and Hsu (1980).

This resource-based approach has advantages over the apparently simpler and more general classical approach for modeling competition. Smale (1976) showed that the equations used in the classical approach, to model competition, can be embedded in an arbitrary system of one dimension higher and hence are compatible with any dynamical behavior provided the number of species is more than three or four, and so do not say much since they do not restrict the possible dynamics. This is not the case for resource-based models of competition (see sections 2.1 and 2.2). Besides this, in the classical models of competition, parameters describing the *carrying capacity* of the environment as well as *competition coefficients* appear. It would be very difficult, if not impossible, to measure these coefficients without growing the competitor populations together. Thus these models tend not to be predictive. On the other hand, the parameters in model (2.1) can be measured by growing each species alone in either batch or continuous culture, and based on the relative sizes of the parameters in the model, the qualitative outcome of mixed-growth competition can be predicted in advance. As well, the predictions can be tested as the predictions in Hsu, Hubbell and Waltman (1976) and Hsu (1978) were tested by Hansen and Hubbell (1980).

2.1 Differential death rates insignificant: $D_i = D$ for all i

In this section we consider model (2.1) under the additional assumption that all of the species specific death rates are insignificant compared to the dilution rate and can be neglected. Thus, we assume that

$$D_i = D \quad \text{for all} \quad i = 1, 2, ..., n. \tag{2.6}$$

We also make the following assumptions of a generic nature:

$$\text{if } \lambda_i \text{ (or } \mu_i) \text{ is finite, then } p_i'(\lambda_i) \neq 0 \ (p_i'(\mu_i) \neq 0); \tag{2.7}$$

$$\text{all } \lambda_i, \mu_j \text{ unless infinite, are distinct from each other and from } S^o. \tag{2.8}$$

Assuming that the populations are labelled so that

$$\lambda_1 < \lambda_2 < \cdots < \lambda_\nu < S^o \leq \lambda_j, \quad \nu + 1 \leq j \leq n, \tag{2.9}$$

where $0 \leq \nu \leq n$, define

$$Q = \bigcup_{i=1}^{\nu} (\lambda_i, \mu_i). \quad (\text{If} \quad \nu = 0, \quad \text{define} \quad Q = \emptyset.)$$

The following results are from Butler and Wolkowicz (1985), and the proofs can be found there.

THEOREM 1 *Assume that (2.2)–(2.4) and (2.6)–(2.9) hold. Let Λ denote the set of left endpoints of components of Q, together with S^o if $S^o \notin Q$. With the exception of a set of initial conditions of Lebesque measure zero, all solutions of (2.1) satisfy*

$$\lim_{t \to \infty} S(t) = \gamma, \quad \gamma \in \Lambda, \tag{2.10}$$

with the corresponding asymptotic behaviour:

$$\text{if } \gamma = \lambda_i \quad \text{then} \quad \lim_{t \to \infty} x_i(t) = y_i(S^o - \lambda_i), \quad \lim_{t \to \infty} x_j(t) = 0, \quad j \neq i, \tag{2.11}$$

$$\text{if } \gamma = S^o \quad \text{then} \quad \lim_{t \to \infty} x_j(t) = 0, \quad j = 1, 2, ..., n. \tag{2.12}$$

Conversely, for each $\gamma \in \Lambda$, there is an open, nonempty set of initial conditions for which the solutions of (2.1) satisfy (2.10)–(2.12).

The following Corollary is an immediate consequence of the above theorem.

COROLLARY 2 *Assume that (2.2)–(2.4) and (2.6)–(2.9) hold. If Q is connected and $S^o \in Q$, then all solutions of (2.1) satisfy, $\lim_{t \to \infty} x_1(t) = y_1(S^o - \lambda_1) \equiv x_1^*$, $\lim_{t \to \infty} x_i(t) = 0$, $i = 2, .., n$, $\lim_{t \to \infty} S(t) = \lambda_1$, that is the equilibrium solution $E_{\lambda_1} = (\lambda_1, x_1^*, 0, ..., 0)$ is globally asymptotically stable with respect to solutions of (2.1) initiating in the interior of the nonnegative cone in $\mathbf{R}^{n+1}$.*

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Note that if $p_1(S)$ is monotone increasing and $\lambda_1 < S^o$ or if $\lambda_1 < S^o < \mu_1$, then Q is connected and Corollary 2 applies. In this case, all but one population washes out, and the only surviving population, the one with the lowest break-even concentration, approaches an equilibrium concentration.

To illustrate these results, consider the following (at least theoretical) application to water purification motivated by the work of Yang and Humphrey (1975) and first described in Butler and Wolkowicz (1985). Suppose that there is a single contaminant, say phenol, in the water supply, and that S^o, the input concentration of phenol is relatively high. Suppose also that certain microorganisms feed on phenol in such a way that phenol is growth-limiting at both high and low concentrations (e.g. Pseudomonas putida and Trichosporon cutaneum). Let A denote an acceptable concentration of phenol in the water supply and assume that $A << S^o$. Suppose that microorganism 1 is harmless and that $\lambda_1 < A$, but $\mu_1 << S^o$. If the initial concentration of phenol in the water supply is relatively high, and population 1 is used alone in an attempt to reduce the phenol level, then it is likely that population 1 would wash out of the system and that the concentration of phenol would approach the unacceptable level S^o. On the other hand, suppose that population n satisfies $A < \lambda_n < S^o < \mu_n$. If population n is used alone, $S(t)$ would approach the value λ_n, an improvement, but this is still unacceptable. However, if populations $2, ..., n-1$ could also be used, where the (λ, μ) intervals overlap in such a way as to form a single component of Q, containing S^o, then regardless of the initial concentrations of the populations (as long as they are positive) $\lim_{t\to\infty} S(t) = \lambda_1 < A$, a tolerable situation.

2.2 Differential death rates significant: An open problem

In this section we summarize what is known about the dynamics of model (2.1) when assumption (2.6) is relaxed.

Using a Lyapunov function of the form:

$$\int_{\lambda_1}^{S} \frac{(p_1(\xi) - D_1)(S^o - \lambda_1)}{D_1(S^o - \xi)} d\xi + \frac{1}{y_1}(x_1 - x_1^* - x_1^*(\ln(x_1) - \ln(x_1^*))) + \sum_{i=2}^{n} \frac{\alpha_i}{y_i} x_i,$$

where α_i, $i = 2, ..., n$ are positive constants and $x_1^* = \frac{y_1 D(S^o - \lambda_1)}{D_1}$, Wolkowicz and Lu (1992) proved the following result.

THEOREM 3 *Assume (2.2)–(2.5) and $\lambda_1 < S^o < \mu_1$. If it is possible to find constants $\alpha_i > 0$ for each $i \geq 2$ satisfying $\lambda_i < S^o$ such that*

$$\max_{0<S<S_1} g_i(S) \leq \alpha_i \leq \min_{\lambda_i < S < \rho_i} g_i(S) \tag{2.13}$$

where

$$g_i(S) = \frac{p_i(S)(-D_1 + p_1(S))(S^o - \lambda_1)}{D_1(-D_i + p_i(S))(S^o - S)}, \quad and \quad \rho_i \equiv \min(\mu_i, S^o),$$

then all solutions of (2.1) satisfy $\lim_{t\to\infty} x_1(t) = x_1^*$, $\lim_{t\to\infty} x_i(t) = 0$, $i = 2, 3, ..., n$, and $\lim_{t\to\infty} S(t) = \lambda_1$, that is the equilibrium solution $E_{\lambda_1} = (\lambda_1, x_1^*, 0, \cdots, 0)$ is globally asymptotically stable with respect to solutions initiating in the interior of the nonnegative cone in $\mathbf{R}^{n+1}$.

In Wolkowicz and Lu (1992) it was also proved that if the response functions were selected in any combination from the four prototypes, the prototypes for monotone response functions: Holling type I, II, or III; or the prototype for nonmonotone response functions: inhibition; described earlier, it is always possible to select constants α_i satisfying (2.13) and so provided that $\lambda_1 < \lambda_2 \leq \cdots \leq \lambda_n$ and $\lambda_1 < S^o < \mu_1$, all but one population washes out, and the only surviving population, the one with the lowest break-even concentration, approaches an equilibrium concentration.

We conjecture that for general response functions that satisfy only (2.2)–(2.3), Theorem 3 holds even if (2.13) is not satisfied and that Theorem 1 holds even if (2.6) is not satisfied, but these remain open problems.

3   PREDICTIONS OF VARIOUS MODELS OF GROWTH WITH RESPECT TO ENRICHMENT OF THE ENVIRONMENT

In this section we consider four different models of population growth and compare what they say about enrichment of the environment.

3.1   Logistic growth – the Verhulst model

Verhulst (1838) proposed the following equation as a model of population growth.

$$x'(t) = rx(t)(1 - \frac{x(t)}{K}). \tag{3.1}$$

where $x(0) > 0$. Here, r denotes the intrinsic growth rate of the population and K denotes the carrying capacity of the environment. He assumed that a self-limiting process operates when a population x at time t becomes too large. This equation has become known as the *logistic* equation for population growth. Provided that $x(0) > 0$, $\lim_{t \to \infty} x(t) = K$. Thus, the carrying capacity is equal to the limiting value of the population size. Since enrichment of the environment is interpreted as increasing the carrying capacity K, this model predicts that increasing the carrying capacity always results in an increase in the population size.

3.2   Growth on a renewable resource: the classical predator-prey model

A predator-prey model can be thought of as a model of growth of a population (the predator) on a renewable resource (the prey). In Rosenzweig (1971), mathematical models of predator-prey interaction of the generalized Gause form

$$
\begin{aligned}
x'(t) &= x(t)g(x(t), K) - yp(x(t)) \\[2mm]
y'(t) &= y(t)(-s + q(x(t)))
\end{aligned}
\tag{3.2}
$$

where $x(0) > 0$ and $y(0) > 0$ were considered. In (3.2), $x(t)$ denotes the size of the prey population (density, biomass or concentration) at time t and $y(t)$ the size of the predator

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population. K denotes the carrying capacity of the environment, s the intrinsic death rate of the predator, $g(x,K)$ the per capita growth rate of the prey in the absence of the predator ($xg(x,K)$ is often modeled by logistic growth), $p(x)$ the predator response function (often modeled by Holling type I, II, or III), and $q(x)$ the conversion rate of prey to predator (also, often Holling type I, II, or III).

Using a local analysis, Rosenzweig showed that sufficient enrichment of the environment supporting the prey species (that is increasing K sufficiently) can cause destabilization of an otherwise stable coexistence equilibrium. Integrating the equations numerically and using a truncation for the sake of biological reality, he obtained extinction of the predator population. Consequently, he issued the following warning. "Man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance."

A number of authors have raised objections to Rosenzweig's results. Gilpin (1972) and May (1972) showed that the destabilization of the coexistence equilibrium can result in the birth of an asymptotically stable periodic orbit. Freedman (1976) showed the destabilization of the equilibrium to be the result of a Hopf bifurcation. Therefore, deterministically, no population is driven to extinction by enrichment of the environment. All solutions approach either the coexistence equilibrium or a surrounding periodic orbit that lies entirely in the interior of the nonnegative cone in $\mathbf{R}^2$. Rosenzweig (1972a, 1972b) argued however, that if the amplitude of the periodic orbit is sufficiently large, a random perturbation could result in the extinction of one or both populations when sections of it come close to the axes. Wolkowicz (1988) proved that depending on the parameters and choice of response functions, the Hopf bifurcation can be either subcritical or supercritical, and pointed out that when it is subcritical there is a parameter range in which there are at least two nontrivial periodic orbits surrounding the interior equilibrium. In this case, there is an asymptotically stable periodic orbit surrounding the coexistence equilibrium before and after its destabilization. It is an unstable periodic orbit that lives between the stable periodic orbit and the stable equilibrium that disappears when there is sufficient enrichment to destabilize the equilibrium by means of a subcritical Hopf bifurcation.

McAllister, LeBrasseur, and Parsons (1972) object to the extrapolation of Rosenzweig's mathematical results to natural ecosystems, providing experimental evidence that moderate enrichment can be beneficial. However, there is experimental evidence in support of Rosenzweig's results. (See, for example, [Huffaker, Shea, and Herman (1963), Luckinbill (1973), Schaffer and Rosenzweig (1978)].) Both sets of experiments are consistent with the predictions of the model discussed in section (3.4). As well, McAllister et al. suggest that Rosenzweig's results might have better been used to prompt questions concerning the critical values of enrichment and how they relate to the other parameters. The model discussed in section (3.4) addresses such issues.

3.3 The single resource growth model in a chemostat

Consider a model of single species growth in a chemostat, that is model (2.1) in the case that $n = 1$. Omitting subscripts, since there is no ambiguity, the model becomes:

$$S'(t) = (S^o - S(t))D - \frac{x(t)p(S(t))}{y},$$

$$x'(t) = x(t)(-\bar{D} + p(S(t))),$$

(3.3)

where $S(0) \geq 0$, $x(0) > 0$, and $S^o, D, \bar{D}$, and y are positive constants.

Using a Lyapunov function of the form:

$$\int_\lambda^S \frac{(p(\xi) - \bar{D})}{p(\xi)} d\xi + \frac{1}{y}(x - x^* - x^*(\ln(x) - \ln(x^*))),$$

where $x^* = yD(S^o - \lambda)/\bar{D}$, the following result can easily be proved using the LaSalle (1960) extension theorem.

THEOREM 4 *Consider model (3.3). Assume (2.2)-(2.4) and either*

(i) $p(S) < \bar{D}$ *for all* $0 \leq S \leq S^o$, *or*

(ii) *there exists* $\lambda > 0$ *such that* $p(S) < \bar{D}$ *if* $0 < S < \lambda$ *and* $p(S) > \bar{D}$ *if* $\lambda < S < S^o$.

If (i) *holds, then the washout equilibirium, $E_o = (S^o, 0)$, is globally asymptotically stable with respect to all solutions initiating in the the nonnegative cone in $\mathbf{R}^2$. If* (ii) *holds, then the survival equilibrium, $E_\lambda = (\lambda, x^*)$, is globally asymptotically stable with respect to all solutions initiating in the interior of the nonnegative cone in $\mathbf{R}^2$.*

Since the equilibrium E_λ is globally asymptotically stable, as in (3.1), it makes sense to identify the carrying capacity of the environment with the equilibrium concentration of the population, that is x^*, and enrichment of the environment with an increase in the input concentration of resource S, that is S^o. This model predicts that if $p(S) \leq \bar{D}$ for all $S > 0$, then enriching the environment will not make any difference to the asymptotic outcome. The population will eventually die out. On the other hand, it predicts that if $p(S) > \bar{D}$ for some $S > 0$, then increasing S^o above λ would prevent extinction of the population and once $S^o > \lambda$, (since x^* increases linearly as S^o increases), it predicts that the carrying capacity of the environment increases linearly with enrichment.

3.4 The two resource growth model in a chemostat

The work summarized in this section is taken from Ballyk and Wolkowicz (1995) and more details as well as the proofs of all of the results can be found there.

A model of single-species growth in the chemostat on two essential, nonreproducing, noninhibitory resources is considered here. With two resources available, it is important to consider how the resources, once consumed, are used by the consumer for growth. Tilman (1982) classifies resources is terms of the shape of the resource dependent growth isoclines, that is the curves representing the amounts of the two resources

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required to yield a given reproductive rate. On the other hand, Rapport (1971) and León and Tumpson (1975) classify resources in terms of consumer needs. It is this latter classification that we adopt in this section. This classification yields a spectrum of resource types. At one extreme are the perfectly substitutable resources. These are resources that are alternate sources of the same essential nutrient. In this case, the rates of consumption of the different resources can be substituted in a fixed ratio in order to maintain a given rate of growth. An example for a bacterium would be two carbon sources or two nitrogen sources. At the other extreme are the complementary resources. In this section, it is assumed that the resources, denoted S and R, are perfectly substitutable for species x. The model is then given by the following system of differential equations:

$$
\begin{aligned}
S'(t) &= (S^o - S(t))D - x(t)\frac{1}{\xi}\mathcal{S}(S(t), R(t)), \\
R'(t) &= (R^o - R(t))D - x(t)\frac{1}{\eta}\mathcal{R}(S(t), R(t)), \\
x'(t) &= x(t)(-D + \mathcal{G}(S(t), R(t))),
\end{aligned}
\tag{3.4}
$$

where $S(0) \geq 0$, $R(0) \geq 0$, $x(0) > 0$, and S^o, R^o, D, ξ and η are positive constants.

For convenience it is assumed that the volume of the culture vessel is one cubic unit. The culture vessel is also assumed to be well-stirred, so that spatial variation need not be considered and nutrients, microorganisms and byproducts are removed in proportion to their concentrations. $x(t)$ denotes the population density at time t. If only one feed bottle is used, S^o and R^o denote the concentrations of resources S and R, respectively, in the feed vessel. All other nutrients are assumed to be supplied at such quantities that these are the only nutrients that limit growth. The constant D is the input rate from the feed vessel to the culture vessel, as well as the washout rate from the culture vessel to the receptacle. Thus constant volume is maintained and the species specific death rate is assumed to be insignificant in comparison to the dilution rate.

The function $\frac{1}{\xi}\mathcal{S}(S, R)$ denotes the rate of consumption of resource S per unit biomass of population x as a function of the concentrations of resources S and R in the growth vessel. The conversion of nutrient to biomass of population x is assumed to be proportional to the amount of nutrient consumed. Thus, $\mathcal{S}(S, R)$ represents the rate of conversion of nutrient S to biomass of population x with corresponding growth yield constant ξ. The relationship between the function $\mathcal{R}(S, R)$ and the constant η is similarly defined.

For the purposes of this paper we restrict our attention to the response functions in Waltman, Hubbell, and Hsu (1980). They are a generalization of the familiar Michaelis-Menten prototype of functional response to a single resource, and are given by

$$
\begin{aligned}
\mathcal{S}(S, R) &= \frac{m_S K_R S}{K_S K_R + K_R S + K_S R}, \\
\mathcal{R}(S, R) &= \frac{m_R K_S R}{K_S K_R + K_R S + K_S R}.
\end{aligned}
$$

Thus, the resources are noninhibitory, since the consumption of each resource is a strictly monotone increasing function of the concentration of that resource. However, increasing the amount of one resource consumed results in a reduction in the amount of the other resource consumed. In Holling terminology, the handling time devoted to the processing

of a unit of one resource is time no longer available for the processing of the other resource. Here, m_S is the maximal growth rate of species x on resource S in the absence of resource R, and K_S is the corresponding half-saturation constant. The constants m_R and K_R are similarly defined.

The function $\mathcal{G}(S, R)$ denotes the rate of conversion of nutrient to biomass of population x as a function of the concentrations of resources S and R in the culture vessel. Since resources S and R are perfectly substitutable, the rate of conversion of nutrient to biomass of population x is made up of a contribution from the consumption of nutrient S as well as a contribution from the consumption of resources R. Therefore,

$$\mathcal{G}(S, R) = \frac{m_S K_R S + m_R K_S R}{K_S K_R + K_R S + K_S R}.$$

Resource S is assumed to be superior to resource R in the sense that

$$m_S \geq m_R.$$

Define

$$\lambda = \begin{cases} \frac{K_S D}{m_S - D} & \text{if } m_S > D, \\ \infty & \text{otherwise,} \end{cases} \quad \text{and} \quad \mu = \begin{cases} \frac{K_R D}{m_R - D} & \text{if } m_R > D, \\ \infty & \text{otherwise,} \end{cases}$$

where λ is obtained by solving the equation $\mathcal{G}(S, 0) = D$ when $m_S > D$ and μ is obtained by solving the equation $\mathcal{G}(0, R) = D$ when $m_R > D$. Thus λ and μ represent the break-even concentrations for resources S and R, respectively, when none of the other resource is available.

It is important to note that neither resource is inherently detrimental. Resources S and R are alternate sources of the same essential nutrient. Therefore, at least one of these resources must be supplied in sufficient amounts in order for the species to survive. Even if only one of the resources (S or R) is supplied, species x would survive provided the dilution rate is sufficiently slow, that is $\lambda < S^o$ or $\mu < R^o$. Then species x could survive on resource S or resource R alone. When either resource is absent, the model actually reduces to model (3.3) with $\mathcal{S}(S, R) = \mathcal{S}(S, 0) = p(S)$ or $\mathcal{R}(S, R)) = \mathcal{R}(0, R))$, that is Holling type II response functions. In this one-resource case, as we saw in section 3.3, the carrying capacity of the environment (given by the species component of the survival equilibrium) is an increasing function of the input concentration of that resource, thus, the higher the input concentration the better.

Define a survival equilibrium of (3.4) to be a solution $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$ of the system

$$\begin{aligned} x\mathcal{S}(S, R) &= \xi(S^o - S)D, \\ x\mathcal{R}(S, R) &= \eta(R^o - R)D, \\ \mathcal{G}(S, R) &= D, \end{aligned}$$

with $\bar{S} \geq 0$, $\bar{R} \geq 0$ and $\bar{x} > 0$.

(left margin fragments) ...g of the other resource. ...the absence of resource ...stants m_R and K_R are

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...$(\bar{S}, \bar{R}, \bar{x})$ of the system

Consider three cases:

I the dilution rate, D, is relatively slow, that is $m_S > D$ and $m_R > D$;

II the dilution rate, D, is relatively fast, that is $m_R \leq m_S \leq D$;

III the dilution rate, D, takes an intermediate speed, that is $m_R < D < m_S$.

CASE I: $m_S > D$ and $m_R > D$.
It can be shown that,

1. A survival equilibrium exists if and only if $\mathcal{G}(S^o, R^o) > D$.

2. If $\mathcal{G}(S^o, R^o) > D$, then there exists a unique survival equilibrium $\bar{E}$, and it is globally asymptotically stable with respect to solutions satisfying $x(0) > 0$.

3. If $\mathcal{G}(S^o, R^o) \leq D$, then the washout equilibrium $E_o = (S^o, R^o)$ is globally asymptotically stable.

In this case, it can also be shown that if $\mathcal{G}(S^o, R^o) \leq D$, then increasing the concentration of either S^o or R^o sufficiently will reverse the inequality and result in the survival of the species. Also, if $\mathcal{G}(S^o, R^o) > D$, enrichment by increasing either S^o or R^o cannot destroy the global stability of the unique survival equilibrium, $\bar{E}$.

As well, identifying the carrying capacity of the environment with the species component of the survival equilibrium, $\bar{x}$, it follows that the carrying capacity is always an increasing function of S^o and of R^o. Thus, enrichment using either resource is always beneficial if the dilution rate is sufficiently slow.

CASE II: $m_R \leq m_S \leq D$.
In this case it can be shown that, the washout equilibrium $E_o = (S^o, R^o)$ is always globally asymptotically stable, regardless of the concentrations of S^o and R^o. Thus, enrichment using either resource cannot prevent the extinction of the species and is a waste of time and effort.

CASE III: $m_R < D < m_S$.
Fix $S^o > \lambda$, since otherwise it can be shown that there is no way to avoid extinction, no matter what the concentration of R^o. For mathematical convenience only, define $\delta = \frac{K_R D}{m_R - D} < 0$. This parameter δ is not intended to denote a resource concentration. Also, define

$$R_1^o = \frac{\delta}{\lambda}(\lambda - S^o),$$

$$R_2^o = \begin{cases} -\delta \dfrac{(\sqrt{\lambda[m_R K_S z - m_S K_R]} - \sqrt{S^o m_R K_S z})^2}{m_S K_R \lambda} & \text{if } \dfrac{\eta}{\xi}\dfrac{m_S K_R}{m_R K_S}\dfrac{S^o}{(S^o - \lambda)} < 1, \\ R_1^o & \text{otherwise,} \end{cases}$$

where $z = \xi/\eta$.

Note that, since $\frac{S^o}{S^o - \lambda} > 1$ is decreasing in S^o for $S^o > \lambda$, if $\frac{\eta m_S K_R}{\xi m_R K_S} \geq 1$, then $R_1^o = R_2^o$ for all $S^o > \lambda$. However, if $\frac{\eta m_S K_R}{\xi m_R K_S} < 1$, then define $S_1^o = \left(\frac{\xi m_R K_S}{\xi m_R K_S - \eta m_S K_R}\right)\lambda$. Clearly $S_1^o > \lambda$. In this case, if $\lambda < S^o < S_1^o$, then $R_2^o = R_1^o$, but if $S^o > S_1^o$, then $R_2^o > R_1^o$.

In Ballyk and Wolkowicz (1995) the following statements were proved.

1. If $0 \leq R^o < R_1^o$, then there exists a unique survival equilibrium $\bar{E}$ of (3.4), and $\bar{E}$ is globally asymptotically stable with respect to all solutions satisfying $x(0) > 0$.

2. If $R_1^o < R^o < R_2^o$, then there exist precisely two survival equilibria for system (3.4). One survival equilibrium is locally asymptotically stable and the other is unstable. The asymptotic behaviour of solutions is initial condition dependent. Any solution either approaches the washout equilibrium, E_o, or approaches a survival equilibrium.

3. If $R^o > R_2^o$, then no survival equilibrium exists, and the washout equilibrium, E_o is globally asymptotically stable.

In this case we will identify the carrying capacity of the environment with the species component of the locally asymptotically stable survival equilibrium, when one exists. The question that remains, is how the species component of the asymptotically stable survival equilibrium is affected by an increase in the input concentration of resources S or R.

Fixing R^o and enriching the environment by increasing S^o is always beneficial. This can be seen by viewing R_1^o as a function of S^o. Fix $S^o > \lambda$ and $R^o > R_1^o(S^o)$. Then, there is either washout or initial condition dependent outcomes. Since $R_1^o(S^o)$ is an increasing function of S^o and $\lim_{S^o \to \infty} R_1^o(S^o) = \infty$, for sufficiently large S^o, $R_1^o(S^o) > R^o$. Once the system enters this regime, there exists a unique survival equilibrium $\bar{E}$ and $\bar{E}$ is globally asymptotically stable with respect to all solutions satisfying $S(0) \geq 0$, $R(0) \geq 0$ and $x(0) > 0$. The species component of this equilibrium and hence the carrying capacity of the environment can also be shown to be an increasing function of S^o.

On the other hand, increasing R^o may or may not be beneficial. In this case, there may be one or two critical values of R^o, $R_1^o \leq R_2^o$. When $0 \leq R^o < R_1^o$, there exists a unique survival equilibrium that is globally asymptotically stable. For $R_1^o < R^o < R_2^o$ the species survives or washes out depending on the initial conditions. Increasing R^o beyond R_2^o leads to extinction.

To see how the carrying capacity of the environment is affected by enrichment, we consider two examples that indicate that moderate enrichment via an increase in R^o can be, but is not always, beneficial. Figures 3.1 and 3.2 are bifurcation diagrams for system (3.4) that exhibit the change in $\bar{x}$ as a function of R^o, for fixed $S^o > \lambda$. The solid curves indicate that the associated equilibrium is asymptotically stable.

In Figure 3.1, the parameter values given in Wolkowicz, Ballyk, and Daoussis (1995) were used. For these parameter values,

$$\frac{\eta}{\xi} \frac{m_S K_R}{m_R K_S} \frac{S^o}{(S^o - \lambda)} \approx 0.32 < 1,$$

and so there are two critical values of R^o: $R_1^o = 0.5$ and $R_2^o \approx 0.7066$. For $0 \leq R^o < R_2^o$, the species component of the locally asymptotically stable survival equilibrium, and hence the carrying capacity of the environment is a decreasing function of R^o. This indicates that even moderate enrichment is detrimental to the species. That this is not always the case, can be seen in the next example.
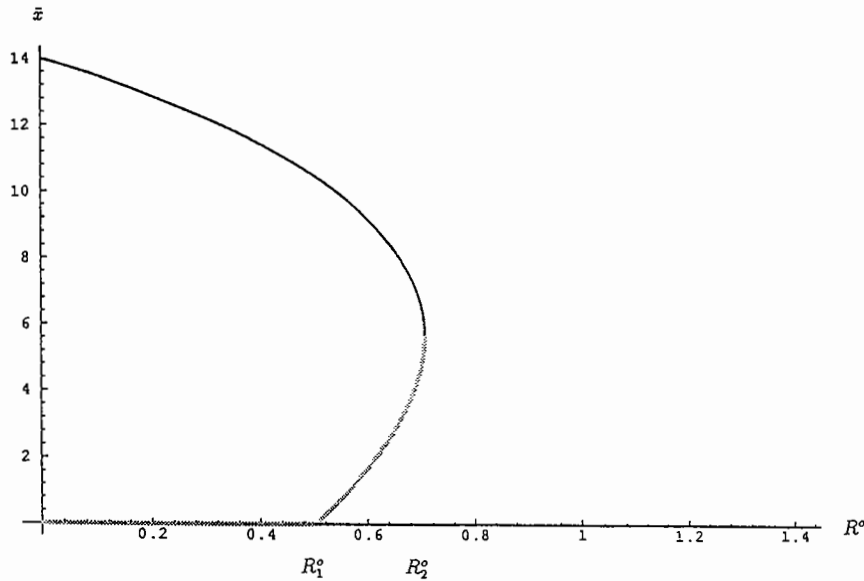
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Figure 3.1 Bifurcation diagram for system (3.4), taking $m_S > D > m_R$ and $S^o > \lambda$. $m_S = 2.25$, $K_S = 1.00$, $\xi = 70$, $m_R = 0.5$, $K_R = 1.00$, $\eta = 1$, $D = 1$, $S^o = 1$.

In Figure 3.2, parameter values that correspond to a facultatively chemolithotrophic *Thiobacilus* species that can grow heterotrophically on acetate (S), autotrophically on thiosulfate (R), and mixotrophically on both were used. (See Gottschal and Thingstad (1982).) Fixing $D = 0.10h^{-1}$, so that $m_S > D > m_R$, it follows that $\lambda \approx 2.22\mu M$. If $S^o = 20.00\mu M$, then

$$\frac{\eta}{\xi}\frac{m_S K_R}{m_R K_S}\frac{S^o}{(S^o - \lambda)} \approx 0.48 < 1.$$

Therefore, as in the previous example, there are two critical values of R^o: $R_1^o \approx 53.33\mu M$ and $R_2^o \approx 78.62\mu M$. There exists $\hat{R}^o \in (R_1^o, R_2^o)$ such that, for $0 < R^o < \hat{R}^o$, the species component of the locally asymptotically stable survival equilibrium is an increasing function of R^o. It is only when R^o is increased beyond $\hat{R}^o$ that the species component of this equilibrium begins to decrease until, for $R^o > R_2^o$, there is washout. Thus, in this case, moderate enrichment using R^o is beneficial, even though too much enrichment is devastating.

More intuitively, since resource S is more nourishing than resource R in the sense that the maximal growth rate on resource S, by assumption, is higher than on resource R, resource R can be thought of as junk food. Even though resource R is adequately sustaining when the dilution rate is sufficiently small, it is not nourishing enough when the dilution rate is high, since the species cannot grow fast enough on it in this case. Its presence also reduces the consumption of the more nourishing resource S, since the species wastes time consuming R. Thus, moderate concentrations of resource R can be beneficial, (see Figure 3.2), but sufficiently high concentrations can cause washout.
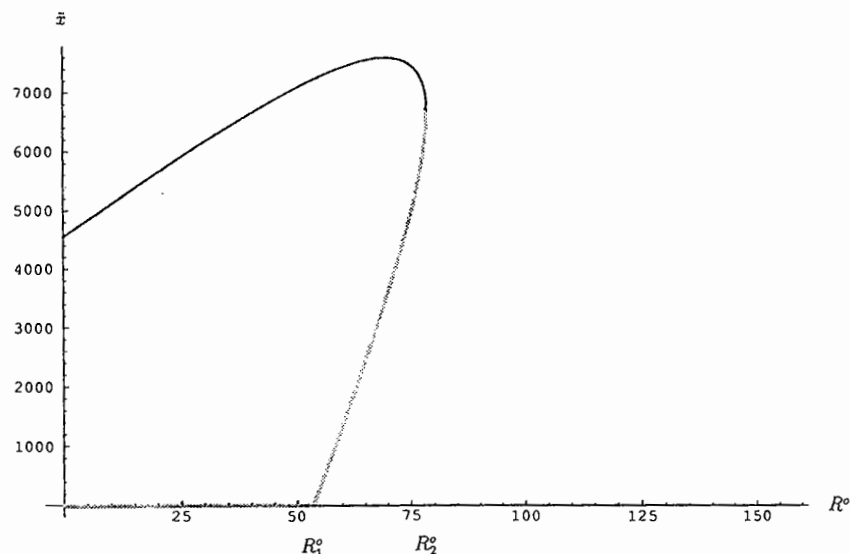
Figure 3.2 Bifurcation diagram for system (3.4), taking $m_S > D > m_R$ and $S^o > \lambda$, $m_S = 0.145h^{-1}$, $K_S = 1.00\mu M$, $\xi = 25.6$ g dry wt/mol, $m_R = 0.085h^{-1}$, $K_R = 1.00\mu M$, $\eta = 6.40$ g dry wt/mol, $D = 0.10h^{-1}$, $S^o = 20.00\mu M$.

We summarize the predictions of the model discussed in this section by considering an application. According to Williams (1971), the chemostat provides a good laboratory idealization of a natural lake system. The lake itself can be thought of as the culture vessel and some population of microorganisms important for the health of the lake could be considered the population x. Natural turnover provides the stirring. Rivers flow in and out of the lake. Asume that two noninhibitory, perfectly substitutable, growth limiting resources are being supplied by the inflowing river. The flow rate is modeled using a constant dilution rate D, in model (3.4) rather than a time-dependent dilution rate $D(t)$. A time-dependent dilution rate may be more appropriate for species at higher trophic levels, where seasonal fluctuations come into play. We feel that a bifurcation approach using a constant dilution rate may actually be a better model for the lower-level microbial species considered here. We are motivated by the shorter generation times typical of such species. (For example, the generation time of species *paramecium aurelia* considered by Luckinbill (1973), is approximately 0.26 days.) Usually the dilution rate remains relatively constant within a season, and the time required for the chemostat to equilibrate is relatively short compared to the length of a season. In order to manage the microbial populations of aquatic systems, this model predicts that it may be necessary to take into consideration when and how much to enrich and to be careful what resource to use. In Canada, in the winter it is very cold. The lakes freeze and there is lots of snow. Thus the chemostat could be thought of as being on hold. In the spring, the ice and snow melt and it rains quite often. The chemostat could be thought of as starting up in the

spring, and due to the spring run-off, the natural dilution rate is relative high. On the other hand, in the summer it is much hotter and dryer and so the dilution rate is relatively small. In the summer it may be that the natural dilution rate satisfies m_S, $m_R > D$, so that enrichment with either resource is beneficial. However, since the natural dilution rate is higher during spring run-off, success with enrichment with a particular resource in the summer can lead to the false conclusion that enriching the environment next year in the spring would be equally beneficial with disastrous consequences. In fact, if the dilution rate is high enough in the spring so that $m_S > D > m_R$, it becomes necessary to consider which resource is used for enrichment. When the superior resource S is used, that is the resource with the larger maximal growth rate, enrichment is always beneficial. However, when the other resource, R, is used, moderate enrichment may or may not be beneficial (see Figures 3.1 and 3.2), and increasing the nutrient input to the system sufficiently could actually lead to total decimation of the population. As well, in any season that $m_S > D > m_R$, success with moderate enrichment (see Figure 3.2) might suggest that more vigorous enrichment would be even more beneficial, again leading to diastrous consequences. Note also (see Figures 3.1 and 3.2) that there is a hysteresis effect. Once R^o is increased beyond R_2^o and the population starts to die out, to remedy the situation, it may not be enough to decrease R^o below R_2^o, but rather it might be necessary to decrease R^o below R_1^o in order to enter the basin of attraction of the aymptotically stable survival equilibrium.

The predictions of model (3.4) seem to provide more support that we should indeed heed Rosenzweig's (1971) warning. The results in this section may also help to explain some of the effects of fertilizer runoff and industrial waste on the microbial populations of certain lakes.

4   DISCUSSION

Perhaps motivated by the methods of Rosenzweig (1971), Brauer (1976) states that "enrichment of the prey's environment ... may be described mathematically by an increase in the carrying capacity." Our results indicate that this is not always the case and suggest that models with the carrying capacity built in, like models (3.1) and (3.2), may be misleading for answering questions related to the effect of enrichment of the environment on the population size.

The results in section 3.4 also seem to indicate that construction of models assuming that only one resource is limiting at a given time may also lead to misleading predictions, especially if the model is to be robust enough to remain valid for reasonable ranges of the parameters. The chemostat model (3.3), for growth on a single, noninhibitory, limiting resource predicts that the outcome is always initial condition independent. If the maximal growth rate of the species is slower than the dilution rate, then enrichment is a waste of time since it cannot prevent extinction of the population. Otherwise, it is always beneficial to enrich by increasing the input concentration of the limiting resource. Raising the input concentration S^o so that $p(S^o) > \bar{D}$ prevents extinction, and once S^o is above the break-even concentration, the population size increases linearly as a function of S^o. However, if there are two perfectly substitutable resources, model (3.4) predicts

that one must consider the relative values of m_S and m_R, the maximal growth rates of species x on resources S and R respectively, and dilution rate D. Assume that resource S is superior to resource R in the sense that $m_S > m_R$. In the case that $m_R \leq m_S \leq D$, enrichment is a waste of time as in the single resource case. Also, in the case that $m_S > D$ and $m_R > D$, as in the single resource model, the outcome is always initial condition independent but to prevent extinction in this case, one only needs to increase S^o or R^o so that $\mathcal{G}(S^o, R^o) > D$. The biggest difference comes in the case that $m_R < D < m_S$. In this case the outcome can be initial condition dependent. There can be two survival equilibria and one of them and the washout equilibrium can be asymptotically stable for the same set of parameters. Enrichment by increasing S^o can lead from washout, to initial condition dependent outcomes, to a globally asymptotically stable survival equilibrium. Enrichment by increasing R^o can lead from a globally asymptotically stable survival equilibrium, to initial condition dependent outcomes with washout a possibility, to definite washout.

For an analysis of models of competition in the multiple resource case the reader is referred to Butler and Wolkowicz (1987) and Ballyk and Wolkowicz (1993) and the references contained in these papers. For a surprising example where competition seems to promote greater diversity the reader is referred to Wolkowicz, Ballyk, and Daoussis (1995). In Ballyk (1994), the thresholds described in section 3.4 of this paper are used to study the effects of enrichment on a resource-based, predator-prey model. For analysis of a model describing the effect of invasion of a predator on competitors in a chemostat the reader is referred to Wolkowicz (1990) and the references within. For two recent books that discuss various models of microbial interactions in the chemostat, the reader is referred to Chen and Chen (1993) and Smith and Waltman (1995).

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