

## **An examination of the thresholds of enrichment: a resource-based growth model**

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**Abstract.** A model of single-species growth in the chemostat on two non-reproducing, growth-limiting, noninhibitory, perfectly substitutable resources is considered. The medium in the growth vessel is enriched by increasing the input concentration of one of the resources. Analytical methods are used to determine the effects of enrichment on the asymptotic behaviour of the model for different dilution rates. It is shown that there exists a threshold value for the dilution rate which depends on the maximal growth rate of the species on each of the resources. Provided the dilution rate is below the threshold, enrichment is beneficial in the sense that the carrying capacity of the environment is increased, regardless of which resource is used to enrich the environment. When the dilution rate is increased beyond the threshold, it becomes important to consider which resource is used for enrichment. For one of the resources it is shown that, while moderate enrichment can be beneficial, sufficient enrichment leads to the extinction of the microbial population. For the other resource, enrichment leads from washout or initial condition dependent outcomes to survival, and is thus beneficial. There are important implications of these results to the management of natural aquatic ecosystems. For example, while enrichment may be beneficial to the microbial species during the summer months, it can lead to their decimation during spring run-off, when the natural dilution rate is higher.

**Key words:** Enrichment threshold – Chemostat – Growth

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## 1 Introduction

In [17], Rosenzweig considers six mathematical models of predator-prey interaction. He shows that sufficient enrichment of the environment supporting the prey species can cause destabilization of an otherwise stable coexistence equilibrium. Integrating his equations numerically and using a truncation for the sake of biological reality, he obtains extinction of the predator population. Consequently, he issues 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 [8] and May [14] show that the destabilization of the coexistence equilibrium results in the birth of an asymptotically stable periodic orbit. Freedman [6] shows the destabilization of the equilibrium to be the result of a Hopf bifurcation. Rosenzweig [18, 19] points out 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.

McAllister, LeBraasseur and Parsons [13] 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. They 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, [10, 12, 20].)

In most of the work dealing with the paradox of enrichment, two-species models are considered. As a very incomplete sample, we mention [1, 4–8, 13, 14, 16, 17, 21, 27]. In this paper we deal with a single-species growth model, and show that enrichment of the system via an increase in the availability of a noninhibitory resource can lead to the extinction of the species. In so doing, we begin to answer some of the questions posed by McAllister et al. [13].

This paper is organized as follows. First, a resource-based model of single-species growth in the chemostat on two growth-limiting, nonreproducing, noninhibitory, perfectly substitutable resources is described. Members of the microbial population are assumed to compete only by decreasing the common pool of resources, so that there is no mutual interference. All species-specific parameters of our model are considered fixed, while the quantities under the control of the experimenter are varied. For a given dilution rate, the environment is enriched by increasing the input concentration of one of the resources. It is then shown that there exists a threshold value for the dilution rate which depends on the maximal growth rate of the species on each of the resources. Provided the dilution rate is below this threshold, enrichment is beneficial in the sense that the carrying capacity of the environment is increased, regardless of which resource is used to enrich the

environment. When the dilution rate is increased beyond the threshold, it becomes important to consider which resource is used for enrichment. For one of the resources it is shown that, while moderate enrichment can be beneficial, sufficient enrichment leads to the extinction of the microbial population. For the other resource, enrichment leads from washout or initial condition dependent outcomes to survival, and is thus beneficial. We conclude the paper with a discussion in which we summarize and interpret our results, and indicate the implications for resource management.

In a following paper [3] the thresholds established here are used to study the effects of enrichment on a resource-based predator-prey model.

## 2 The model

The model considered here is motivated by the example given by Wolkowicz, Ballyk and Daoussis in [26] and is an example of the one-species growth submodels treated by Ballyk and Wolkowicz in [2]. A more detailed description can be found in [2].

We consider a model of single-species growth in the chemostat on two essential, nonreproducing resources. With two resources available it is important to consider how the resources, once consumed, are used by the consumer for growth. Rapport [15] and León and Tumpson [11] classify resources in terms of consumer needs. This classification yields a spectrum of resource types. For example, perfectly substitutable resources 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. We will assume that the resources, denoted  $S$  and  $R$ , are perfectly substitutable for species  $x$ .

The function  $\frac{1}{\xi} \mathcal{S}(S, R)$  will represent 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. We assume that the conversion of nutrient to biomass of population  $x$  is 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  $\xi$ . The relationship between the function  $\mathcal{R}(S, R)$  and the constant  $\eta$  is similarly defined.

For the purposes of this paper we restrict our attention to the response functions in Waltman, Hubbell and Hsu [24]. They are a generalization of the familiar Michaelis-Menten prototype of functional response to a single resource, and are given by

$$\begin{aligned} \mathcal{S}(S, R) &= \frac{m_S K_R S}{K_S K_R + K_R S + K_S R}, \\ \mathcal{R}(S, R) &= \frac{m_R K_S R}{K_S K_R + K_R S + K_S R}. \end{aligned} \tag{1}$$

Thus, the resources are noninhibitory, as 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  $\mathcal{G}(S, R)$  will represent 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,

$$\mathcal{G}(S, R) = \frac{m_S K_R S + m_R K_S R}{K_S K_R + K_R S + K_S R}. \quad (2)$$

The model is now given by the following system of differential equations:

$$\begin{aligned} S'(t) &= (S^\circ - S(t))D - x(t)\frac{1}{\xi}\mathcal{S}(S(t), R(t)), \\ R'(t) &= (R^\circ - R(t))D - x(t)\frac{1}{\xi}\mathcal{R}(S(t), R(t)), \\ x'(t) &= x(t)(-D + \mathcal{G}(S(t), R(t))), \\ S(0) &\geq 0, R(0) \geq 0, x(0) \geq 0. \end{aligned} \quad (3)$$

We identify  $(S, R, x)$ -space with  $R_+^3 = \{(S, R, x): S, R, x \geq 0\}$ . We have 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. If only one feed bottle is used,  $S^\circ$  and  $R^\circ$  are the concentrations of resources  $S$  and  $R$ , respectively, in the feed vessel. 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.

We will assume that resource  $S$  is superior to resource  $R$  in the sense that

$$m_S \geq m_R. \quad (4)$$

When the inequality in (4) is strict, the partial derivatives of  $\mathcal{G}(S, R)$  satisfy the following conditions:

$$\begin{aligned} \frac{\partial}{\partial S} \mathcal{G}(S, R) &> 0 \quad \text{for all } (S, R) \in \text{int} \mathbf{R}_+^2, \\ \frac{\partial}{\partial R} \mathcal{G}(S, R) &> 0 \quad \text{for all } R > 0, 0 < S < S^c, \\ \frac{\partial}{\partial R} \mathcal{G}(S, R) &< 0 \quad \text{for all } R > 0, S > S^c, \end{aligned} \tag{5}$$

where  $S^c = m_R K_S / (m_S - m_R)$  is related to  $m_R$  in the following manner:

$$\mathcal{G}(S^c, R) = m_R \quad \text{for all } R \geq 0. \tag{6}$$

Note that if  $m_S = m_R$ , then we define  $S^c = \infty$ .

Thus, when both resources are in relatively short supply, increasing the concentration of either resource is beneficial. Once resource  $S$  is plentiful enough that  $m_R$  would be exceeded by consuming only resource  $S$ , the presence of resource  $R$  could actually become detrimental. However,

$$\lim_{R \rightarrow \infty} \mathcal{G}(S, R) = m_R \quad \text{for each fixed } S \geq 0, \tag{7}$$

so that the presence of resource  $R$  would never be detrimental enough to decrease  $\mathcal{G}(S, R)$  below  $m_R$ . Since an abundance of  $S$  and no  $R$  would be optimal for the growth of population  $x$ ,  $m_S$  can never be exceeded, so that

$$\lim_{S \rightarrow \infty} \mathcal{G}(S, R) = m_S \quad \text{for each fixed } R \geq 0.$$

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

Note that if the dilution rate is slow enough so that  $\lambda < S^\circ$  ( $\mu < R^\circ$ ), then species  $x$  could survive on resource  $S$  (respectively,  $R$ ) alone and the higher  $S^\circ$  (respectively,  $R^\circ$ ), the better. (See, for example, [23].) In this respect, neither resource is inherently detrimental.

For system (3), the coordinate plane in which species  $x$  is absent is invariant. If  $S(\bar{t}) = 0$  (respectively,  $R(\bar{t}) = 0$ ) for some  $\bar{t}$ , then  $S'(\bar{t}) = S^\circ D > 0$  (respectively,  $R'(\bar{t}) = R^\circ D > 0$ ). From this, and the uniqueness of initial value problems, it follows that  $\text{int} \mathbf{R}_+^3$  is positively invariant for solutions of (3). Further, by considering  $z(t) = \xi S(t) + \eta R(t) + x(t)$  it follows from (3) that the simplex

$$\mathcal{M} = \{(S, R, x) \in \mathbf{R}_+^3 : \xi S + \eta R + x = \xi S^\circ + \eta R^\circ\} \tag{8}$$

is a global attractor. Thus, all solutions are positive and bounded.

Define a survival equilibrium of (3) to be a solution  $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$  of the system

$$x\mathcal{S}(S, R) = \xi(S^\circ - S)D, \tag{9}$$

$$x\mathcal{R}(S, R) = \eta(R^\circ - R)D, \tag{10}$$

$$\mathcal{G}(S, R) = D, \tag{11}$$

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

First consider the case where the dilution rate,  $D$ , is relatively small.

**Lemma 2.1.** Consider (3). Suppose that  $m_S \geq D, m_R \geq D$ , and  $\mathcal{G}(S^\circ, R^\circ) > D$ .

(a) There exists a unique survival equilibrium  $\bar{E}$  and  $\bar{E}$  is globally asymptotically stable with respect to all solutions for which  $S(0) \geq 0, R(0) \geq 0$ , and  $x(0) > 0$ .

(b)

$$\mathcal{G}(\bar{S}^\circ, R^\circ) > D \text{ for any } \bar{S}^\circ > S^\circ, \tag{12}$$

and

$$\mathcal{G}(S^\circ, \bar{R}^\circ) > D \text{ for any } \bar{R}^\circ > R^\circ. \tag{13}$$

(c) The species component of the survival equilibrium,  $\bar{x}$ , is a strictly increasing function of both  $S^\circ$  and  $R^\circ$ .

*Proof.* Since  $\mathcal{G}(S^\circ, R^\circ) > D$  implies that at least one of the inequalities,  $m_S \geq D$  or  $m_R \geq D$ , must be strict, without loss of generality, assume  $m_S > D, m_R \geq D$ , and  $m_S \geq m_R$ .

(a) Lemma 2.1 is Theorem 3.9(a) of [2] and a proof can be found there.

(b) (12) follows immediately by (5). If  $S^\circ < S^c$ , then (13) follows immediately from (5). If  $S^\circ \geq S^c$ , since  $m_R \geq D$ , the result follows from (5)–(7).

(c) Note that  $\lambda \leq S^c$ , with equality if and only if  $m_R = D$ . By (5),

$$D = \mathcal{G}(\lambda, 0) \leq \mathcal{G}(\lambda, R) < \mathcal{G}(\hat{S}, R) \text{ for any } \hat{S} > \lambda.$$

Therefore,

$$\mathcal{G}(S, R) = D \text{ implies that } S \leq \lambda \leq S^c, \tag{14}$$

with  $S = \lambda = S^c$  if and only if  $m_R = D$ .

First we prove that  $\bar{x}$  is a strictly increasing function of  $R^\circ$ . The proof to show that  $\bar{x}$  is a strictly increasing function of  $S^\circ$  is similar. For  $S^\circ = S_*^\circ$  and  $R^\circ = R_*^\circ$  satisfying  $\mathcal{G}(S_*^\circ, R_*^\circ) > D$ , let  $\bar{E}_* = (\bar{S}_*, \bar{R}_*, \bar{x}_*)$  denote the unique survival equilibrium, and for  $S^\circ = S_*^\circ$  and  $R^\circ = R_\varepsilon^\circ = R_*^\circ + \varepsilon$  for an arbitrary  $\varepsilon > 0$ , let  $\bar{E}_\varepsilon = (\bar{S}_\varepsilon, \bar{R}_\varepsilon, \bar{x}_\varepsilon)$  denote the unique survival equilibrium (guaranteed by parts (a) and (b)). It suffices to show that  $\bar{x}_\varepsilon > \bar{x}_*$ . Suppose instead that  $\bar{x}_\varepsilon \leq \bar{x}_*$ .

Then  $\bar{R}_\varepsilon < \bar{R}_*$  is impossible, since (11) implies that  $\mathcal{G}(\bar{S}_\varepsilon, \bar{R}_\varepsilon) = D = \mathcal{G}(\bar{S}_*, \bar{R}_*)$ , and so by (14) and (5), if  $\bar{R}_\varepsilon < \bar{R}_*$ , then  $\bar{S}_\varepsilon \geq \bar{S}_*$ . But

then, by (10),  $\eta(R_*^\circ - \bar{R}_*)D = \bar{x}_* \mathcal{R}(\bar{S}_*, \bar{R}_*) > \bar{x}_\varepsilon \mathcal{R}(\bar{S}_\varepsilon, \bar{R}_\varepsilon) = \eta(R_\varepsilon^\circ - \bar{R}_\varepsilon)D > \eta(R_*^\circ - \bar{R}_*)D$ , a contradiction.

$\bar{R}_\varepsilon \geq \bar{R}_*$  is also impossible, since then (11), (14), and (5) imply that  $\bar{S}_\varepsilon \leq \bar{S}_*$ . But then, by (9),  $\zeta(S_*^\circ - \bar{S}_*)D \leq \zeta(S_*^\circ - \bar{S}_\varepsilon)D = \bar{x}_\varepsilon \mathcal{S}(\bar{S}_\varepsilon, \bar{R}_\varepsilon) \leq \bar{x}_* \mathcal{S}(\bar{S}_\varepsilon, \bar{R}_\varepsilon) \leq \bar{x}_* \mathcal{S}(\bar{S}_*, \bar{R}_*) = \zeta(S_*^\circ - \bar{S}_*)D$ , with at least one strict inequality yielding a contradiction, unless  $m_R = D$  and hence, by (9), and (14)  $\bar{x}_\varepsilon = \bar{x}_*$ ,  $\bar{R}_\varepsilon = \bar{R}_*$ , and  $\bar{S}_\varepsilon = \bar{S}_*$ . But then, by (10),  $\eta(R_\varepsilon^\circ - \bar{R}_*)D > \eta(R_*^\circ - \bar{R}_*)D = \bar{x}_* \mathcal{R}(\bar{S}_*, \bar{R}_*) = \bar{x}_\varepsilon \mathcal{R}(\bar{S}_\varepsilon, \bar{R}_\varepsilon) = \eta(R_\varepsilon^\circ - \bar{R}_\varepsilon)D = \eta(R_\varepsilon^\circ - \bar{R}_*)D$ , again a contradiction.

Therefore,  $\bar{x}_\varepsilon \leq \bar{x}_*$  is impossible and the result follows. □

Thus, if  $m_S \geq D$ ,  $m_R \geq D$ , and  $\mathcal{G}(S^\circ, R^\circ) > D$ , enrichment by increasing either  $S^\circ$  or  $R^\circ$  cannot destroy the global stability of the unique survival equilibrium,  $\bar{E}$ . Also, 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 both  $S^\circ$  and  $R^\circ$ . Thus, provided the dilution rate is sufficiently slow, enrichment using either resource is always beneficial.

We now consider what happens when the dilution rate  $D$  is increased so that  $m_S > D > m_R$ . For mathematical convenience only, we define

$$\delta = \frac{K_R D}{m_R - D} < 0 ; \tag{15}$$

$\delta$  is not intended to denote a resource concentration. Note that

$$\lambda = \frac{K_S D}{m_S - D} > \frac{K_S m_R}{m_S - m_R} = S^c . \tag{16}$$

Setting  $\mathcal{G}(S, R) = D$  and solving for  $R$  we obtain

$$\mathcal{G}(S, \varphi(S)) = D \quad \text{for all } S \geq \lambda ,$$

where

$$\varphi(S) = \frac{\delta}{\lambda}(\lambda - S) \quad \text{for all } S \geq \lambda . \tag{17}$$

Then the curve  $\varphi(S)$  gives the concentrations of  $S$  and  $R$  at which the biomass of population  $x$  in the culture vessel is neither increasing nor decreasing.

We begin by examining the existence of equilibria of system (3) when  $m_S > D > m_R$ . The washout equilibrium,  $E^\circ = (S^\circ, R^\circ, 0)$ , always exists. A standard linear analysis shows that  $E^\circ$  is unstable whenever  $\mathcal{G}(S^\circ, R^\circ) > D$  and is locally asymptotically stable whenever  $\mathcal{G}(S^\circ, R^\circ) < D$ . Any other critical points of (3) must be survival equilibria. Note that if a survival equilibrium of the form  $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$  exists, then, by (9), (10), (11), (17), and the positivity constraint on  $\bar{x}$ ,

$$\lambda < \bar{S} < S^\circ . \tag{18}$$

The following theorem examines the existence of survival equilibria as a function of  $R^\circ$ , the input concentration of resource  $R$ . Clearly  $S^\circ > \lambda$  is a necessary condition for the existence of a survival equilibrium.

**Theorem 2.2.** Consider system (3). Assume  $m_S > D > m_R$  and fix  $S^\circ > \lambda$ . Define

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

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

where  $z = \xi/\eta$ .

(a) If  $0 \leq R^\circ < R_1^\circ$ , then there exists a unique survival equilibrium  $\bar{E}$  of (3).

(b) If  $R^\circ > R_2^\circ$ , then no survival equilibrium exists.

(c) If  $R_1^\circ < R^\circ < R_2^\circ$ , then there exist precisely two survival equilibria for system (3).

*Proof.* Note that  $\frac{\eta m_S K_R}{\xi m_R K_S} \frac{S^\circ}{(S^\circ - \lambda)} < 1$  implies that  $m_R K_{SZ} - m_S K_R > 0$ , so that  $R_2^\circ$  is well-defined. If  $R^\circ = 0$ , then it follows immediately from (3) that the unique survival equilibrium is given by  $\bar{E} = (\lambda, 0, \xi(S^\circ - \lambda))$ .

If an equilibrium of the form  $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$  exists for  $R^\circ > 0$ , then it follows from (11) that  $\bar{R} = \varphi(\bar{S})$ , where  $\varphi(S)$  is as in (17). From (9) and (10), define

$$x_S(S) \triangleq \frac{\xi(S^\circ - S)D}{\mathcal{F}(S, \varphi(S))} \quad \text{and} \quad x_R(S, R^\circ) \triangleq \frac{\eta(R^\circ - \varphi(S))D}{\mathcal{R}(S, \varphi(S))}$$

for  $R^\circ \geq 0$ . Note that  $x_S(\bar{S}) = x_R(\bar{S}, R^\circ)$  where, by (18),  $\lambda < \bar{S} < S^\circ$ . By (1), (16), and (17),  $x_S(S) = x_R(S, R^\circ)$  if and only if

$$f(S, R^\circ) \triangleq [R^\circ - \varphi(S)]S = \frac{\xi \delta m_R K_S}{\eta \lambda m_S K_R} (S^\circ - S)(\lambda - S) \triangleq g(S).$$

By (15) and (17),  $f(S, R^\circ)$  and  $g(S)$  are parabolas opening downward for each  $R^\circ \geq 0$ . Fixing  $R^\circ$  and setting  $f(S, R^\circ) = 0$  we find that  $S = 0$  or

$$S = \hat{S}(R^\circ) \triangleq \frac{\lambda}{\delta}(\delta - R^\circ).$$

Note that  $\hat{S}(0) = \lambda$ ,  $\hat{S}(R^\circ) > 0$  and  $\hat{S}(R^\circ) \leq S^\circ$  if and only if  $R^\circ \leq R_1^\circ$ , and  $g(S) \geq 0$  for all  $S \in [\lambda, S^\circ]$ . Therefore, to each  $R^\circ \in (0, R_1^\circ)$  there corresponds a unique  $\bar{S} \in (\lambda, S^\circ)$  such that  $f(\bar{S}, R^\circ) = g(\bar{S})$ . This proves (a).

Consider  $R^\circ = R_1^\circ$ . Noting that  $\hat{S}(R_1^\circ) = S^\circ$ , we find that

$$f(S, R_1^\circ) = g(S) \text{ whenever } S = S^\circ \text{ or } S = \frac{\xi m_R K_S}{\xi m_R K_S - \eta m_S K_R} \lambda,$$

where

$$\lambda < \frac{\xi m_R K_S}{\xi m_R K_S - \eta m_S K_R} \lambda < S^\circ \text{ if and only if } \frac{\eta m_S K_R}{\xi m_R K_S} \frac{S^\circ}{(S^\circ - \lambda)} < 1.$$

Since  $\frac{\partial}{\partial R^\circ} f(S, R^\circ) = S$ , parts (b) and (c) now follow. See Fig. 1. □



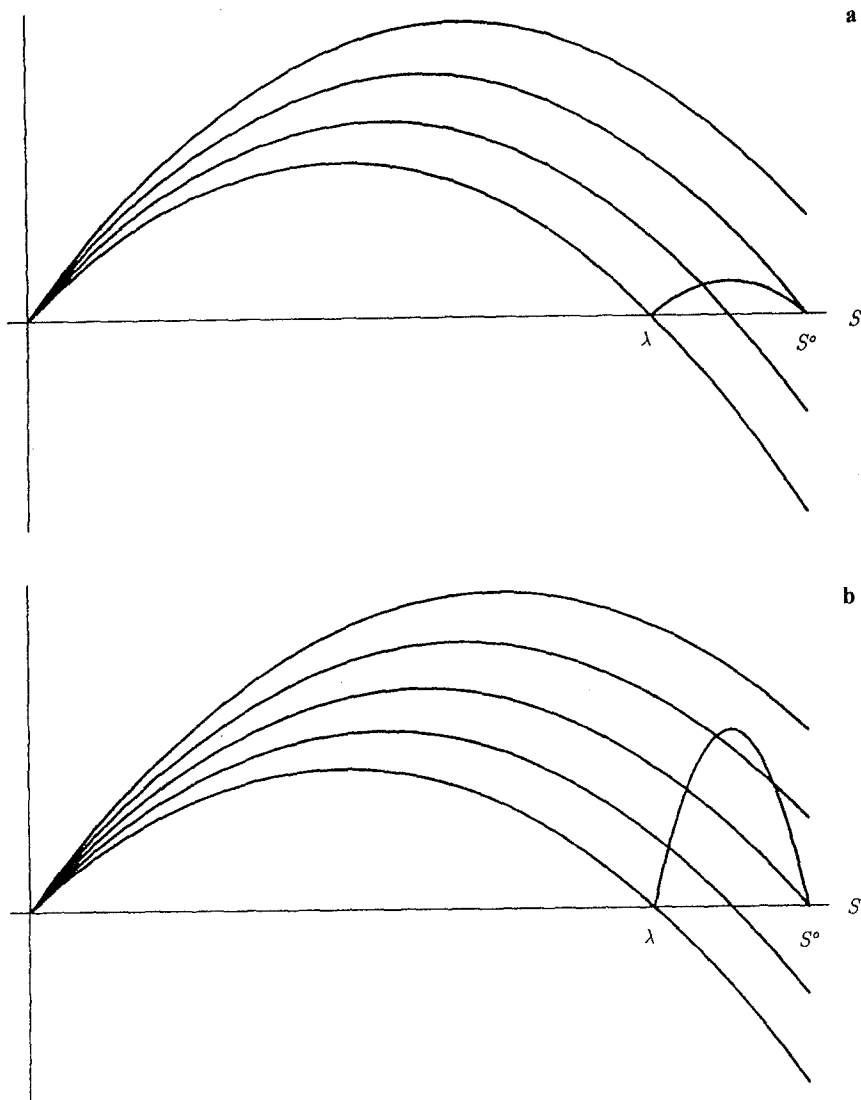


Fig. 1a, b. Schematic diagram for Theorem 2.2: depicts interaction of  $g(s)$  and  $f(S, R^0)$  as  $R^0$  varies.

$$\mathbf{a} \quad \frac{\eta m_S K_R}{\xi m_R K_S} \frac{S^0}{(S^0 - \lambda)} \geq 1 \quad \mathbf{b} \quad \frac{\eta m_S K_R}{\xi m_R K_S} \frac{S^0}{(S^0 - \lambda)} < 1$$

In each of **a** and **b**, the parabolas with roots 0 and  $\lambda$  correspond to  $f(S, 0)$ , i.e.  $R^0 = 0$  while the parabolas with roots 0 and  $S^0$  correspond to  $f(S, R_1^0)$ , i.e.  $R^0 = R_1^0$

*Remark:* Since  $(S^0 / (S^0 - \lambda)) > 1$  is decreasing in  $S^0$  for  $S^0 > \lambda$ , if  $\eta m_S K_R / \xi m_R K_S \geq 1$ , then  $R_1^0 = R_2^0$  for all  $S^0 > \lambda$ .

However, if  $\eta m_S K_R / \xi m_R K_S < 1$ , then define  $S_1^0 = (\xi m_R K_S / (\xi m_R K_S - \eta m_S K_R)) \lambda$ . Clearly  $S_1^0 > \lambda$ . In this case, if  $\lambda < S^0 < S_1^0$ , then  $R_2^0 = R_1^0$ , but if  $S^0 > S_1^0$ , then  $R_2^0 > R_1^0$ .

We now examine the global properties of system (3) when  $m_S > D > m_R$ . The following lemmas will be used in the proof of Theorem 2.5. Lemma 2.3 gives conditions under which species  $x$  survives, while Lemma 2.4 gives conditions under which species  $x$  cannot avoid extinction.

**Lemma 2.3.** *Consider system (3). Suppose  $\mathcal{G}(S^\circ, R^\circ) > D$  and  $x(0) > 0$ . Then*

$$\liminf_{t \rightarrow \infty} x(t) > 0 .$$

**Lemma 2.4.** *Consider system (3). If no survival equilibrium  $\bar{E}$  exists, then  $E^\circ$  is globally asymptotically stable with respect to all solutions for which  $S(0) \geq 0$ ,  $R(0) \geq 0$ , and  $x(0) \geq 0$ .*

Lemmas 2.3 and 2.4 are Theorems 3.8 and 3.9(b), respectively, of [2] and their proofs can be found there. We now show that enriching the environment by increasing  $R^\circ$  leads to the extinction of the population when  $m_S > D > m_R$ .

**Theorem 2.5.** *Consider system (3). Assume  $m_S > D > m_R$  and fix  $S^\circ > \lambda$ . Let  $R_1^\circ$  and  $R_2^\circ$  be defined as in Theorem 2.2.*

- (a) *If  $0 \leq R^\circ < R_1^\circ$ , then there exists a unique survival equilibrium  $\bar{E}$  and  $\bar{E}$  is globally asymptotically stable with respect to all solutions for which  $S(0) \geq 0$ ,  $R(0) \geq 0$ , and  $x(0) > 0$ .*
- (b) *If  $R^\circ > R_2^\circ$ , then  $E^\circ$  is globally asymptotically stable with respect to all solutions for which  $S(0) \geq 0$ ,  $R(0) \geq 0$ , and  $x(0) \geq 0$ .*
- (c) *If  $R_1^\circ < R^\circ < R_2^\circ$ , then the asymptotic behaviour of system (3) is initial condition dependent. Any solution either approaches  $E^\circ$  or approaches a survival equilibrium.*

*Proof.* (a) The existence and uniqueness of  $\bar{E}$  is given by Theorem 2.2(a). We first note that, by (17),  $\mathcal{G}(S^\circ, R_1^\circ) = D$ . By (5) and (16),  $\mathcal{G}(S^\circ, R^\circ) > D$  for all  $0 \leq R^\circ < R_1^\circ$ , so that  $E^\circ$  is unstable. Also, by Lemma 2.3,  $\liminf_{t \rightarrow \infty} x(t) > 0$ .

We restrict our attention to the globally attracting simplex  $\mathcal{M}$  given in (8). Since  $\mathcal{M}$  is positively invariant, let  $x(t) = \xi(S^\circ - S(t)) + \eta(R^\circ - R(t))$  and consider the system

$$\begin{aligned}
 S'(t) &= (S^\circ - S(t))D - \frac{1}{\xi}[\xi(S^\circ - S(t)) + \eta(R^\circ - R(t))]\mathcal{S}(S(t), R(t)) , \\
 R'(t) &= (R^\circ - R(t))D - \frac{1}{\eta}[\xi(S^\circ - S(t)) + \eta(R^\circ - R(t))]\mathcal{R}(S(t), R(t)) , \quad (19)
 \end{aligned}$$

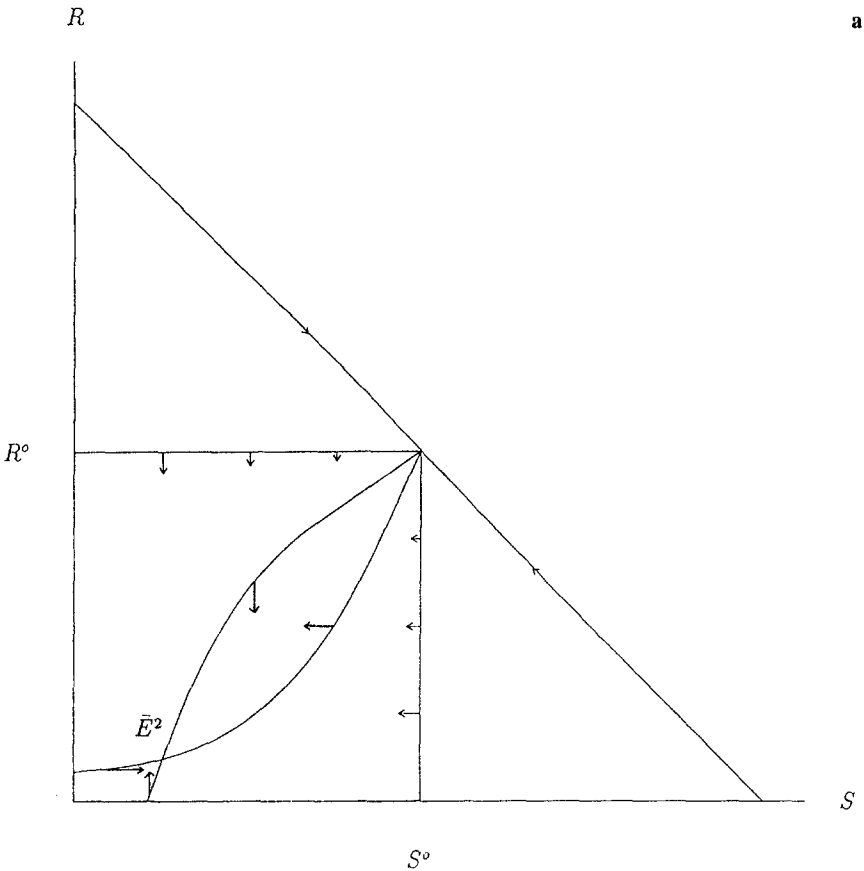
$$S(0) \geq 0, R(0) \geq 0, \xi(S^\circ - S(0)) + \eta(R^\circ - R(0)) \geq 0 .$$

Since  $0 \leq R^\circ < R_1^\circ$ , there are precisely two equilibria for a system (19),  $E^\circ = (S^\circ, R^\circ)$  and  $\bar{E}^2 = (\bar{S}, \bar{R})$  where the superscript 2 indicates the two-dimensional system (19). Sample isoclines and a partial vector field for (19) are shown in Fig. 2(a). (A derivation of the form of the isoclines can be found in the Appendix.) Noting the direction that solutions must cross the isoclines we

conclude that no periodic orbits exist on  $\mathcal{M}$ . Since  $\liminf_{t \rightarrow \infty} x(t) > 0$ , it follows from the Poincaré–Bendixson Theorem that  $\bar{E}^2$  is globally asymptotically stable for system (19) with respect to all solutions for which  $S(0) \geq 0$ ,  $R(0) \geq 0$ , and  $\xi(S^\circ - S(0)) + \eta(R^\circ - R(0)) > 0$ . It follows from Theorem 1.5 of [22] that  $\bar{E} = (\bar{S}, \bar{R}, \bar{x})$ , where  $\bar{x} = \xi(S^\circ - \bar{S}) + \eta(R^\circ - \bar{R})$ , is in the omega limit set of any solution of (3) with  $S(0) \geq 0$ ,  $R(0) \geq 0$ ,  $\eta$ , and  $x(0) > 0$ . Since  $\bar{E}$  is locally asymptotically stable,  $\bar{E}$  is the only point in the omega limit set and so it must be globally asymptotically stable for (3) with respect to all solutions for which  $S(0) \geq 0$ ,  $R(0) \geq 0$ , and  $x(0) > 0$ .

(b) The result follows from Theorem 2.2(b) and Lemma 2.4.

(c) We again restrict our attention to  $\mathcal{M}$  and consider system (19). Since  $R_1^\circ < R^\circ < R_2^\circ$ , there are precisely three equilibria for system (19), two of which correspond to interior equilibria of system (3), by Theorem 2.2(c). The equilibria will be denoted  $E^\circ = (S^\circ, R^\circ)$  and  $\bar{E}_i^2 = (\bar{S}_i, \bar{R}_i)$ ,  $i = 1, 2$ . The isoclines, equilibria, and a partial vector field for (19) are shown in Fig. 2(b).



**Fig. 2.** a Partial vector field for Theorem 2.5(a). b Partial vector field for Theorem 2.5(c). Vectors parallel to the  $S$  axis indicate the sign of  $S'(t)$  along the indicated line. Vectors parallel to the  $R$  axis indicate the sign of  $R'(t)$  along the indicated line

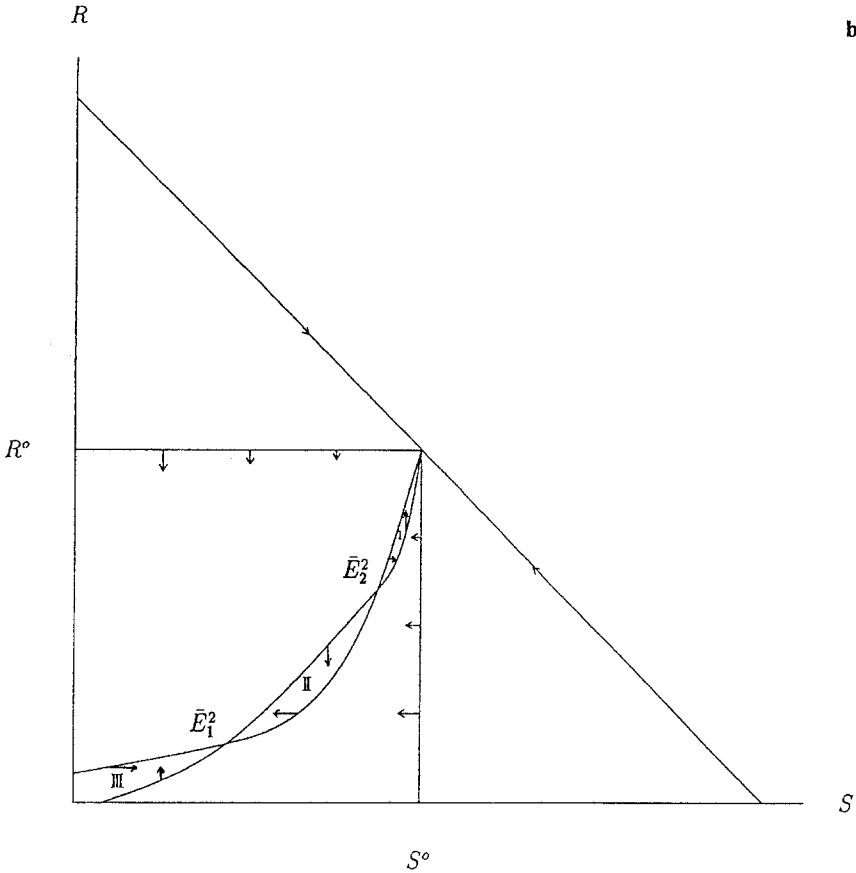


Fig. 2 (continued)

(The reader is again referred to the Appendix for a derivation of the form of the isoclines.) Noting the direction that solutions must cross the isoclines we conclude that there can be no periodic orbits. All solutions initiating off the stable manifold of  $\bar{E}_2^2$  must eventually enter region I, II or III. By the Poincaré–Bendixson Theorem, those entering regions II and III approach  $\bar{E}_1^2$  while those entering region I approach  $E^0$ . Thus  $\bar{E}_1^2$  and  $E^0$  are locally asymptotically stable while  $\bar{E}_2^2$  is a saddle. It follows from Theorem 1.5 of [22] that  $(S_1, R_1, x_1)$  and  $(S^0, R^0, 0)$  are locally asymptotically stable while  $(S_2, R_2, x_2)$  is unstable with two-dimensional stable manifold. (Here  $x_i = \xi(S^0 - S_i) + \eta(R^0 - R_i)$ ,  $i = 1, 2$ .) Therefore, whether the species survives or washes out depends on the initial conditions when  $R_1^0 < R^0 < R_2^0$ .  $\square$

We are now prepared to offer the following bifurcation analysis of system (3), for  $m_S > D > m_R$  and fixed  $S^0 > \lambda$ , based on the parameter  $R^0$ . In all of the bifurcation diagrams (see Figs. 3–5), the solid curves indicate asymptotic stability of the associated equilibria. There are two cases to consider.

**Case 1:** 
$$\frac{\eta m_S K_R}{\xi m_R K_S} \frac{S^\circ}{(S^\circ - \lambda)} \geq 1.$$

When  $R^\circ = 0$  the survival equilibrium  $\bar{E} = (\lambda, 0, \xi(S^\circ - \lambda))$  in the  $R = 0$  plane is globally asymptotically stable. The critical point  $E^\circ$ , corresponding to total washout, exists and is unstable. As  $R^\circ$  is increased, so that  $0 < R^\circ < R_1^\circ$ ,  $\bar{E}$  enters the positive cone, maintaining its stability. When  $R^\circ = R_1^\circ$ ,  $\bar{E}$  and  $E^\circ$  coalesce (see Fig. 1(a)) and the washout equilibrium is globally asymptotically stable. As  $R^\circ$  is increased above  $R_1^\circ$ ,  $\bar{E}$  leaves the nonnegative cone and loses its stability to  $E^\circ$ , so that, for all  $R^\circ > R_1^\circ$ ,  $E^\circ$  is globally asymptotically stable. Thus there is a transcritical bifurcation at  $R^\circ = R_1^\circ$ . See Fig. 3(a).

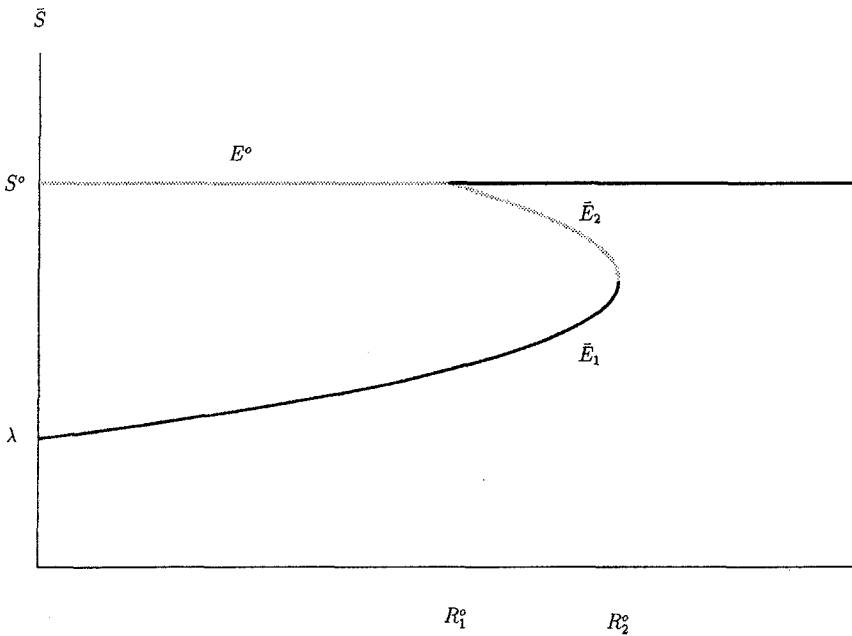
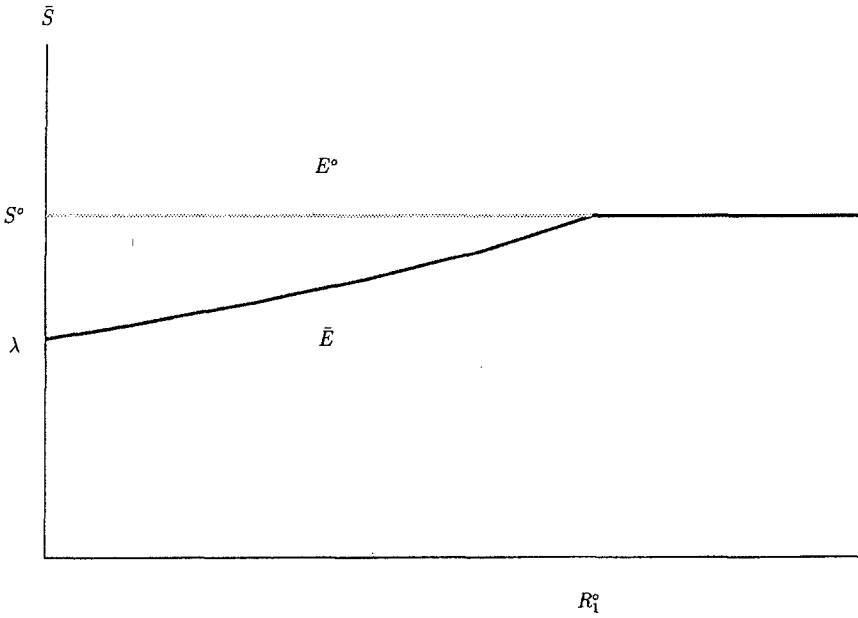
**Case 2:** 
$$\frac{\eta m_S K_R}{\xi m_R K_S} \frac{S^\circ}{(S^\circ - \lambda)} < 1.$$

For  $0 \leq R^\circ < R_1^\circ$ ,  $E^\circ$  and the survival equilibrium  $\bar{E}_1$  behave as above. The second survival equilibrium,  $\bar{E}_2$ , cannot exist in the nonnegative cone. (See Fig. 1(b).) When  $R^\circ = R_1^\circ$ ,  $E^\circ$  and  $\bar{E}_1$  coalesce. As  $R^\circ$  is increased, so that  $R_1^\circ < R^\circ < R_2^\circ$ ,  $\bar{E}_2$ , a saddle, enters the positive cone while  $E^\circ$  and  $\bar{E}_1$  are locally asymptotically stable. Thus we have initial condition dependent outcomes with the stable manifold of  $\bar{E}_2$  acting as the separatrix. When  $R^\circ = R_2^\circ$ ,  $\bar{E}_1$  and  $\bar{E}_2$  coalesce, resulting in a saddle-node. If  $R^\circ$  is increased so that  $R^\circ > R_2^\circ$ ,  $\bar{E}_1$  and  $\bar{E}_2$  no longer exist and  $E^\circ$  is globally asymptotically stable. Thus there is a saddle-node bifurcation at  $R^\circ = R_2^\circ$ . See Fig. 3(b). Note the hysteresis effect in Fig. 3(b). If the input concentration of resources  $R$  exceeds  $R_2^\circ$ , the biomass in the culture vessel decreases. If the quantity of species is very low, the input concentration must be decreased below  $R_1^\circ$  before extinction can be avoided.

The question that remains is how the species component of the survival equilibria are affected by an increase in the input concentration of resource  $R$ . Figure 4 is the bifurcation diagram for system (3) exhibiting the change in  $\bar{x}$  as a function of  $R^\circ$ . In Fig. 4(a) we used the parameter values given in [26]:  $K_S = 1 = K_R$ ,  $m_S = 2.25$ ,  $m_R = 0.5$ ,  $D = 1$ ,  $S^\circ = 1$ ,  $\xi = 70$ , and  $\eta = 1$ . Then

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

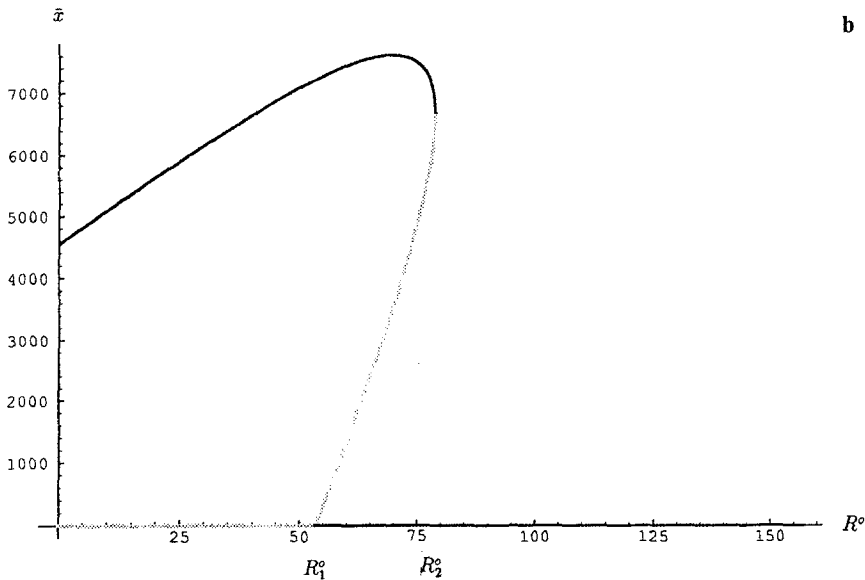
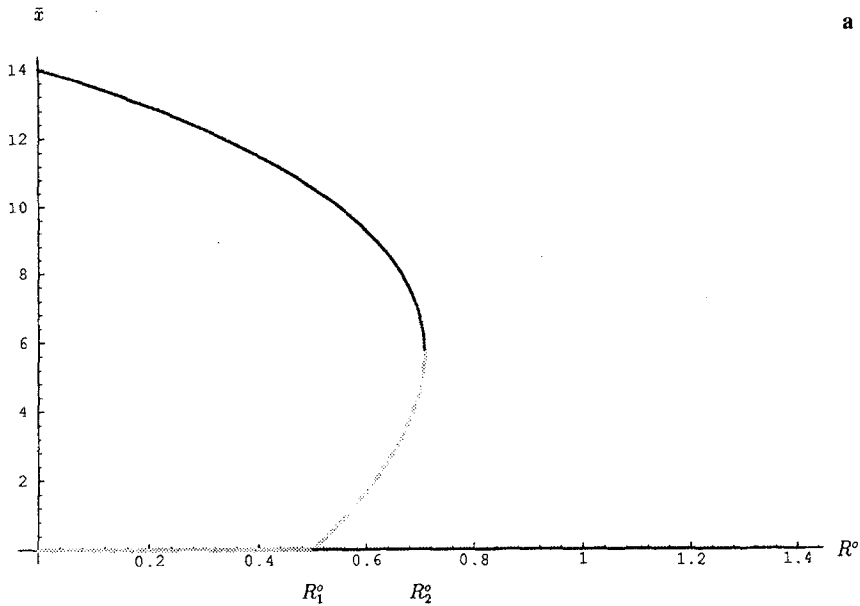
Thus there are two critical values of  $R^\circ$ :  $R_1^\circ = 0.5$  and  $R_2^\circ \approx 0.7066$ . For  $0 \leq R^\circ < R_1^\circ$ , the carrying capacity of the environment is a decreasing function of  $R^\circ$ . For  $R_1^\circ < R^\circ < R_2^\circ$ , the species component of the locally asymptotically stable survival equilibrium is also a decreasing function of  $R^\circ$ . This would indicate that even moderate enrichment is detrimental to the species. However, this is not always the case.



**Fig. 3a, b.** Bifurcation diagrams  $R^{\circ}$  vs  $\bar{S}$  for system (3) where  $m_S > D > m_R$  and  $S^{\circ} > \lambda$ .

**a**  $\frac{\eta m_S K_R}{\zeta m_R K_S} \frac{S^{\circ}}{(S^{\circ} - \lambda)} \geq 1$       **b**  $\frac{\eta m_S K_R}{\zeta m_R K_S} \frac{S^{\circ}}{(S^{\circ} - \lambda)} < 1$ .

Note that values of  $\bar{S}$  satisfying  $\bar{S} < \lambda$  correspond to  $\bar{R} < 0$ , while values of  $\bar{S}$  satisfying  $\bar{S} > S^{\circ}$  correspond to  $\bar{x} < 0$



**Fig. 4a, b.** Bifurcation diagrams  $R^\circ$  vs  $\bar{x}$  for system (3) where  $m_S > D > m_R$  and  $S^\circ > \lambda$ .  
**a**  $m_S = 2.25$ ,  $K_S = 1.00$ ,  $\zeta = 70$ ,  $m_R = 0.5$ ,  $K_R = 1.00$ ,  $\eta = 1$ ,  $D = 1$ ,  $S^\circ = 1$ .  
**b**  $m_S = 0.145 h^{-1}$ ,  $K_S = 1.00 \mu M$ ,  $\zeta = 25.6$  g dry wt/mol,  $m_R = 0.085 h^{-1}$ ,  $K_R = 1.00 \mu M$ ,  
 $\eta = 6.40$  g dry wt/mol,  $D = 0.10 h^{-1}$ ,  $S^\circ = 20.00 \mu M$

In Fig. 4(b) we used the following parameter values. The growth parameters are  $m_S = 0.145 h^{-1}$ ,  $K_S = 1.00 \mu M$ ,  $\zeta = 25.6$  g dry wt/mol,  $m_R = 0.085 h^{-1}$ ,  $K_R = 1.00 \mu M$ , and  $\eta = 0.640$  g dry wt/mol. (These values correspond to a facultatively chemolithotrophic *Thiobacillus* sp. which can

grow heterotrophically on acetate ( $S$ ), autotrophically on thiosulfate ( $R$ ), and mixotrophically on both. See [9].) Fixing  $D = 0.10h^{-1}$ , so that  $m_S > D > m_R$ , we have  $\lambda \approx 2.22 \mu M$ . If  $S^\circ = 20.00 \mu M$ , then

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

Again, there are two critical values of  $R^\circ$ :  $R_1^\circ \approx 53.33 \mu M$  and  $R_2^\circ \approx 78.62 \mu M$ . For  $0 \leq R^\circ < R_1^\circ$ , the carrying capacity of the environment is an increasing function of  $R^\circ$ . Also, there exists  $\hat{R}^\circ \in (R_1^\circ, R_2^\circ)$  such that, for  $R_1^\circ < R^\circ < \hat{R}^\circ$ , the species component of the locally asymptotically stable survival equilibrium is an increasing function of  $R^\circ$ . It is only when  $R^\circ$  is increased beyond  $\hat{R}^\circ$  that the species component of this equilibrium begins to decrease until, for  $R^\circ > R_2^\circ$ , we have washout. Thus, in some cases, moderate enrichment can be beneficial.

We note that, when  $m_S > D > m_R$ , enriching the environment by increasing  $S^\circ$ , the input concentration of resource  $S$ , is beneficial. This can be seen by viewing  $R_1^\circ$  as a function of  $S^\circ$ . Fix  $S^\circ > \lambda$  and  $R^\circ > R_1^\circ(S^\circ)$ . Then, by Theorem 2.5(b, c), we either have washout or initial condition dependent

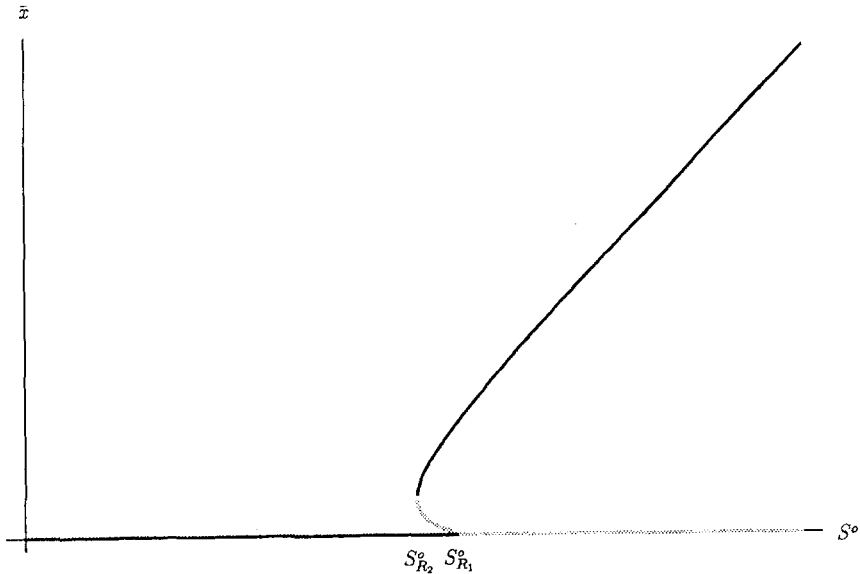


Fig. 5. Bifurcation diagram  $S^\circ$  vs  $\bar{x}$  for system (3) where  $m_S > D > m_R$  and  $\frac{\eta m_S K_R}{\xi m_R K_S} < 1$

$$S_{R_1}^\circ = \left( 1 - \frac{(m_R - D)K_S}{(m_S - D)K_R} R^\circ \right) \lambda$$

$$S_{R_2}^\circ = \frac{\left( \sqrt{\lambda [m_R K_{SZ} - m_S K_R]} - \sqrt{\frac{-R^\circ m_S K_R \lambda}{\delta}} \right)^2}{m_R K_{SZ}}$$



outcomes. Since  $R_1^{\circ}(S^{\circ})$  is an increasing function of  $S^{\circ}$  and  $\lim_{S^{\circ} \rightarrow \infty} R_1^{\circ}(S^{\circ}) = \infty$ , one eventually has  $R_1^{\circ}(S^{\circ}) > R^{\circ}$ . By Theorem 2.5(a) it follows that 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  $x(0) > 0$ . Once the system enters this regime, the carrying capacity of the environment is an increasing function of  $S^{\circ}$ . (See Fig. 5).

Finally, we note that if the dilution rate satisfies  $D \geq m_S \geq m_R$ , then  $E^{\circ}$  is globally asymptotically stable for system (3), regardless of the input concentrations of the resources. This follows from equations (1), (2) and (11), and Lemma 2.4.

### 3 Discussion

In this paper we consider a resource-based model of single-species growth in the chemostat on two growth-limiting, nonreproducing, noninhibitory, perfectly substitutable resources,  $S$  and  $R$ . We do not allow for mutual interference, so that the members of the microbial population compete only by depleting the common pool of resources. Except for  $S^{\circ}$  and  $R^{\circ}$ , the input concentrations of the resources, and  $D$ , the input and washout rate, all parameters of the model are fixed. Therefore, all species-specific parameters are fixed while the quantities under the control of the experimenter are varied.

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. In fact, in this one-response case, 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.

If there are two perfectly substitutable resources, our results seem to indicate that using a model in which only one resource is assumed to be limiting can result in misleading predictions, if the model is to be robust enough to remain valid for reasonable ranges of the parameters. In the two resource case 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  $D$ . We assume that resource  $S$  is superior to resource  $R$  in the sense that  $m_S > m_R$ , so that there is a critical value,  $S^c$ , for resource  $S$ . If the concentration of resource  $S$  is below this critical value, an increase in the concentration of either resource is beneficial. However, once the concentration of resource  $S$  is above this critical value, the presence of resource  $R$  actually can become detrimental.

First, assume that the dilution rate does not exceed the maximal growth rate on either resource, so that  $m_R \geq D$ , and equate enrichment of the environment with an increase in the input concentration of one resource. In this case,  $\mathcal{G}(S^{\circ}, R^{\circ}) > D$  is necessary and sufficient to ensure that a unique survival equilibrium exists and is globally asymptotically stable with respect to the

interior of  $(S, R, x)$ -space. Moreover, the carrying capacity of the environment is an increasing function of both input concentrations. Thus, provided the input rate is sufficiently slow, enriching the environment by increasing  $S^\circ$  or  $R^\circ$  is beneficial.

If  $D$  is increased, so that  $m_S > D > m_R$ , the scenario changes dramatically. First, equate enrichment of the environment with an increase in the input concentration of resource  $R$ . In this case, we identify two critical values of  $R^\circ$ ,  $R_1^\circ \leq R_2^\circ$ , where

$$R_1^\circ < R_2^\circ \quad \text{if and only if} \quad \frac{\eta m_S K_R}{\xi m_R K_S} \frac{S^\circ}{(S^\circ - \lambda)} < 1.$$

When  $0 \leq R^\circ < R_1^\circ$ , there exists a unique survival equilibrium that is globally asymptotically stable. For  $R_1^\circ < R^\circ < R_2^\circ$  the species survives or washes out depending on the initial conditions. Increasing  $R^\circ$  beyond  $R_2^\circ$  leads to extinction. Thus we provide more support that Rosenzweig's [17] warning is valid. We give two examples which indicate that moderate enrichment via an increase in the input concentration of resource  $R$  can be, but is not always, beneficial in the sense that the carrying capacity of the environment is increased. However, enriching the environment by increasing the input concentration of resource  $S$  is beneficial. If  $R^\circ > R_1^\circ$ , increasing  $S^\circ$  leads from washout or initial condition dependent outcomes with washout possible to survival. Once the system enters this regime, the carrying capacity of the environment is an increasing function of  $S^\circ$ .

Why should increasing the input concentration of resource  $R$  lead to extinction when  $m_S > D > m_R$ ? Consider all concentrations  $\bar{S}, \bar{R}$  of resources  $S$  and  $R$  satisfying  $\mathcal{G}(\bar{S}, \bar{R}) = D$ . The concentration  $\bar{S}$  of resource  $S$  is above the critical value  $S^\circ$ . For any fixed  $S > S^\circ$ , the growth rate,  $\mathcal{G}(S, R)$  is a decreasing function of resource  $R$ . One would expect that the faster resource  $R$  is depleted, the better. However, when  $R^\circ > R_2^\circ$ ,

$$\frac{(R^\circ - \bar{R})D}{(S^\circ - \bar{S})D} > \frac{\frac{1}{\eta} \mathcal{R}(\bar{S}, \bar{R})}{\frac{1}{\xi} \mathcal{S}(\bar{S}, \bar{R})}.$$

Thus, the ratio of the net supply rate of resource  $R$  to that of resource  $S$  exceeds the ratio of the consumption rate of resource  $R$  to that of resource  $S$ . As species  $x$  cannot deplete resource  $R$  quickly enough, no survival equilibrium exists.

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 Fig. 4(b)), but sufficiently high concentrations can cause washout.

Perhaps motivated by the methods of Rosenzweig [17], Brauer [4] states that “enrichment of the prey’s environment . . . may be described mathematically by an increase in the carrying capacity.” For dilution rates below the threshold, the results of our resource-based study would support this relationship between enrichment of the prey’s environment and the carrying capacity. However, for dilution rates above the threshold, the validity of this relationship depends on the resource used to enrich the environment. For the superior resource the relationship remains valid. (See Fig. 5.) However, it can only hold for moderate enrichment when the inferior resource is used. (See Figs. 4(a) and 4(b).)

We stress that we have considered a constant dilution rate  $D$ , rather than a time-dependent dilution rate  $D(t)$ . The latter 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 approximation 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 the prey species *paramecium aurelia* considered by Luckinbill [12] 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.

The importance of single-species microbial population dynamics to ecology is beautifully detailed by Williams [25]. In the same study he asserts that the chemostat provides a good laboratory idealization of nature. Our results may provide important implications for the management of aquatic systems. In managing the microbial populations of such systems, it may be necessary to take into consideration when and how much to enrich. 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, the natural dilution rate is higher during spring run-off. Success with enrichment in the summer can lead to the false conclusion that enriching the environment in the spring will be equally beneficial. In fact, if the dilution rate is high enough so that  $m_S > D > m_R$ , it becomes necessary to consider which resource is used for enrichment. When the superior resource is used, enrichment is beneficial. When the inferior resource is used, moderate enrichment can be beneficial, while increasing the nutrient input to the system sufficiently actually leads to washout.

The results in this paper may also help to explain some of the effects of fertilizer runoff and industrial waste on the microbial populations of certain lakes.

#### 4 Appendix: the isoclines of (19)

In this section we examine the general shape of the isoclines for system (19). First, consider the case  $R_1^\circ < R^\circ < R_2^\circ$ . Since  $[(\eta/\xi)(m_S K_R/m_R K_S) \times (S^\circ/(S^\circ - \lambda))] < 1$  and  $m_S > D > m_R$ ,  $[(\eta/\xi)(m_S K_R/(DK_S))] < 1$  and

$[(\xi/\eta)(m_R K_S / (DK_R))] > 1$ . Setting  $S' = 0$  in (19) and solving for  $R$  we obtain

$$\Phi(S) = K_\phi \left\{ \frac{S^2 + a_\phi S + b_\phi}{S - c_\phi} \right\},$$

where

$$a_\phi = - \left\{ \frac{\eta m_S R^\circ}{\xi DK_S} \lambda + \lambda + S^\circ \right\} < 0, \quad b_\phi = S^\circ \lambda > 0,$$

$$c_\phi = S^\circ \left( 1 - \frac{\eta m_S K_R}{\xi DK_S} \right)^{-1} > S^\circ,$$

and

$$K_\phi = \frac{K_R}{\lambda} \left( 1 - \frac{\eta m_S K_R}{\xi DK_S} \right)^{-1} > 0.$$

Similarly, setting  $R' = 0$  in (19) and solving for  $S$  we obtain

$$\Sigma(R) = K_\Sigma \left\{ \frac{R^2 + a_\Sigma R + b_\Sigma}{R - c_\Sigma} \right\},$$

where

$$a_\Sigma = - \left\{ \frac{\xi m_R S^\circ}{\eta DK_R} \delta + \delta + R^\circ \right\}, \quad b_\Sigma = R^\circ \delta < 0,$$

$$c_\Sigma = R^\circ \left( 1 - \frac{\xi m_R K_S}{\eta DK_R} \right)^{-1} < 0,$$

and

$$K_\Sigma = \frac{K_S}{\delta} \left( 1 - \frac{\xi m_R K_S}{\eta DK_R} \right)^{-1} > 0.$$

Note that  $\Phi(0) = -K_R$  and  $\Sigma(0) = -K_S$ .

Both  $\Phi(S)$  and  $\Sigma(R)$  are of the form

$$f(x) = K \frac{x^2 + ax + b}{x - c}, \quad K > 0,$$

so that both functions have slant asymptote with positive slope. For each, the graph is either convex for  $x < c$  and concave for  $x > c$ , as in Figure 6(a), or concave for  $x < c$  and convex for  $x > c$ , as in Figure 6(b).

First, consider  $\Phi(S)$ . The vertical asymptote occurs at  $S = c_\phi > S^\circ$ . By Theorem 2.2(c) the points  $\bar{E}_i^2 = (S_i, R_i)$ ,  $i = 1, 2$ , and  $(S^\circ, R^\circ)$  lie on  $\Phi(S)$ . Since the  $\bar{E}_i^2$  lie on the line  $\varphi(S)$ , given by (17), and  $R^\circ > \varphi(S^\circ) = R_1^\circ$ ,  $\Phi(S)$  must be convex on the interval  $(-\infty, c_\phi)$  as in Fig. 6(a). Similarly, the curve  $\Sigma(R)$  must be concave on the interval  $(c_\Sigma, \infty)$ , as in Fig. 6(a), where  $c_\Sigma < 0$ . Therefore, for  $R_1^\circ < R^\circ < R_2^\circ$  the isoclines of (19) are as in Fig. 2(b).

For  $0 \leq R^\circ \leq R_1^\circ$ , the precise shape of the isoclines cannot be stated, since there is insufficient information to determine the concavity of the corresponding functions  $\Phi(S)$  and  $\Sigma(R)$ . There are nine possible pairings, one of which is

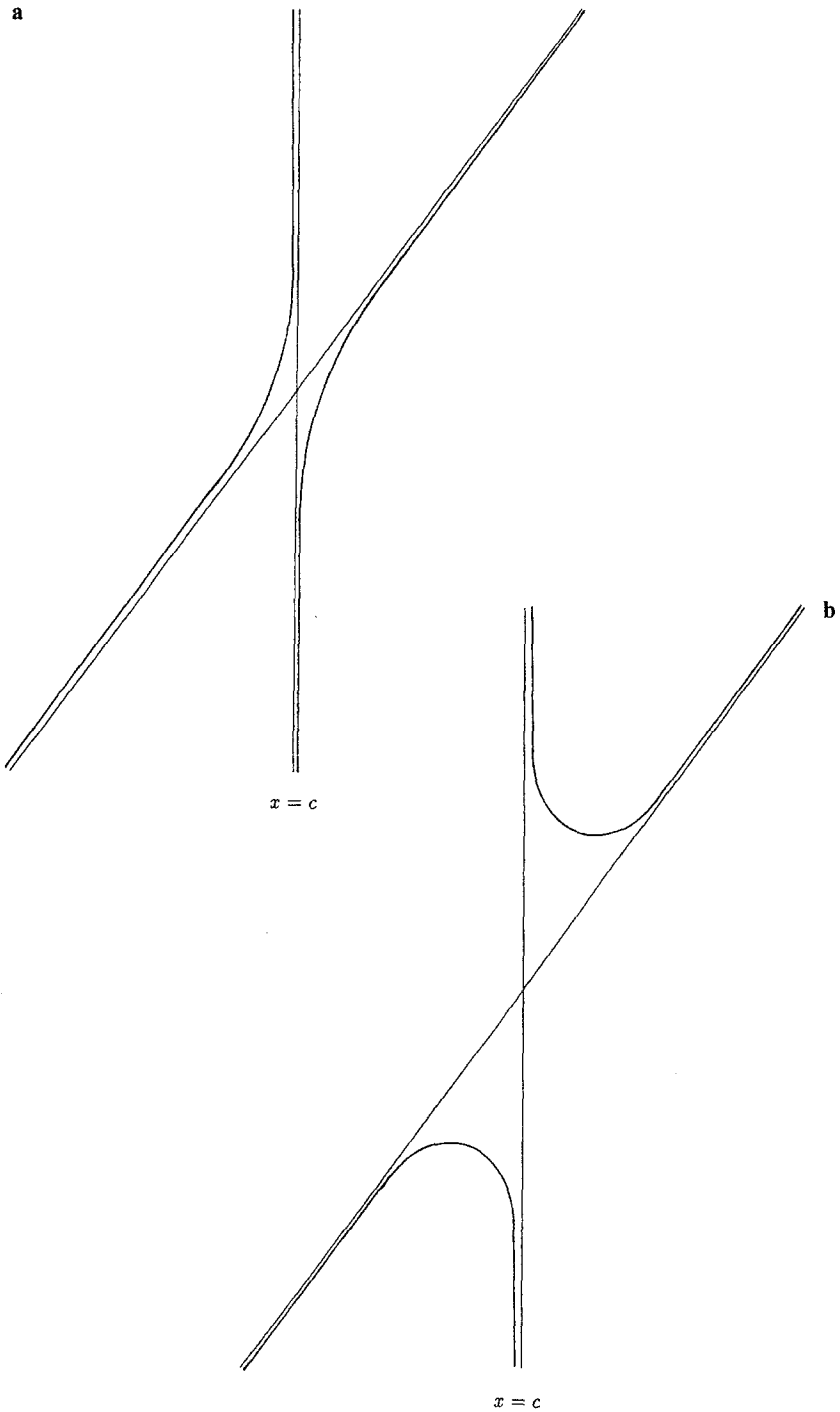


Fig. 6a, b. Schematic diagram for the nullclines of system (19)

depicted in Figure 2(a). However, regardless of the concavity, the asymptotic behaviour of system (3) for  $0 \leq R^o < R_1^o$  is determined as in Theorem 2.5(a).

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