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Predator-mediated competition in the chemostat

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1. Introduction

The chemostat is a laboratory apparatus used for the continuous culture of microorganisms and is helpful for the study of microbial growth under nutrient limitation in a controlled environment. In a more speculative vein, it is also useful as a guide for identifying the dynamical nature of some of the population interactions that might be present in a more complex system such as a lake.

There are many articles devoted to the study of the chemostat both from the experimental and the modelling point of view; as a very incomplete sample of these, we mention [1, 12, 20, 21, 24, 29, 31, 41, 42, 44, 45]. Here we content ourselves with recalling that in its simplest form, the chemostat provides a system in which populations of microorganisms compete in a growth chamber for a single, essential, growth-limiting nutrient which is supplied continuously from a feed bottle in growth-limiting amounts at a constant rate and removed at the same rate together with proportional amounts of microorganisms, by-products and other growth medium to preserve the volume of the system.

If the system is modelled by means of a dynamical system in which the nutrient-uptake for each microorganism is a monotone increasing function of the nutrient density, it is known [2, 5, 21] that at most one of the competing populations will survive. Indeed, even when the monotonicity requirements are relaxed, to model for example, inhibition at high nutrient concentrations, it has been shown that at most one competitor can be maintained in the system [5]; in this case, the successful population may be determined by the initial configuration of the system. Such results of competitive exclusion are also borne out by experiment [20, 47].

In this paper, we introduce a predator population and restrict our attention to the case of only two competitors. We are able to show that this entire food web can be made to persist. We also consider the food chain that results if one of the competing populations is absent from the system. We attempt to unify the mathematical work already done for these problems. Many of our results are of

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a global nature and are for general monotone nutrient-uptake functions. We do however, give results for specific prototypes where this is appropriate.

In addition to obtaining persistence results, we address the related ecological question of whether or not the invasion by a predator can reverse the outcome of competition. The answer depends upon whether one interprets our results purely deterministically or whether one allows for stochastic influences. Our results also help to confirm the current ecological thinking, based on much experimental evidence, (see for example Slobodkin [38] and Paine [32]) that predation is often responsible for the diversity in ecosystems. Paine postulates: "*Local species diversity is directly related to the efficiency with which predators prevent monopolization of the major environmental requisites by one species.*"

A central concept, in our discussion is the notion of persistence, and it is appropriate to give some precise definitions. Several different definitions appear in the literature [6, 15, 16, 19, 22] and we offer three of these below. First it will be convenient to introduce an autonomous system of ordinary differential equations suitable for a general discussion of population dynamics.

Let $f=(f_1, f_2, \ldots, f_n)$ be a continuously differentiable function from $\mathbb{R}^n$ to $\mathbb{R}^n$ such that

$$f_i(w) \geqslant 0 \quad \text{whenever } w=(w_1, \ldots, w_n) \text{ satisfies } w_i=0 \text{ and } w_j \geqslant 0 \qquad (j \neq i).$$

Consider the system

$$w'(t)=f(w(t)); \qquad w_i(0)>0, \qquad i=1, \ldots, n. \tag{1.1}$$

The conditions on f guarantee that (1.1) defines a dynamical system which leaves the positive cone in $\mathbb{R}^n$ positively invariant (necessary if we are dealing with a model of population dynamics).

Definition 1.1: The system (1.1) is *weakly persistent* if for all solutions we have $\overline{\lim}_{t\to\infty} w_i(t)>0$, $i=1, \ldots, n$.

Definition 1.2: The system (1.1) is *persistent* if for all solutions we have $\underline{\lim}_{t\to\infty} w_i(t)>0$, $i=1, \ldots, n$.

Definition 1.3: The system (1.1) is *uniformly persistent* if there exists $\varepsilon_0>0$ such that for all solutions we have $\underline{\lim}_{t\to\infty} w_i(t) \geqslant \varepsilon_0$.

From the point of view of population dynamics, uniform persistence may be regarded as the most desirable form of persistence since in the long run, it provides all populations in the system with a uniform "cushion" away from extinction.

Our paper is organized in the following manner. In Sect. 2 we set down the mathematical model of the food web that we wish to study and we outline the underlying assumptions. An equivalent nondimensional version of this model is then given in Sect. 3 where we also define several important parameters and introduce notation for the critical points of this system. It is this nondimensional version of the model that we actually analyze. In sect. 4 we introduce notation for the three dimensional subsystems that result if one of the competitors or the predator is omitted.

Sections 5 through 9 contain mathematical results. We state and prove preliminary results in Sect. 5. In Sect. 6, we show that for general monotone dynamics, there is a chain of transference of global stability from one regime in the system to another as certain parameters are decreased. For certain prototypes this takes place in a particularly simple fashion as the global stability is handed down from one equilibrium point to another in a sequence of bifurcations. (So [40] gives a similar result for the classical Lotka-Volterra food chain.) In Sect. 7, we consider the food chain that results if the inferior rival is eliminated from the model. We determine conditions that ensure uniform persistence of the entire food web in Sect. 8. The persistence of the entire food web can be considered predator-mediated, since in the absence of the predator at least one of the competitors always becomes extinct. This predator-mediated coexistence is highlighted in the example in Sect. 9 where we also show that invasion by a predator can in some sense reverse the outcome of pure competition.

We conclude the paper with Sect. 10 in which we summarize our results, interpret them with respect to the original model described in Sect. 2, and finally consider the ecological ramifications. For completeness we summarize the local stability analysis of the food web and of the food chain in Appendix A. Part of the linear analysis has already appeared in the literature (see for example Canale [7] and Saunders and Bazin [36]).

Throughout this paper we shall use the following notation:

$\mathcal{O}(P)$ will denote the orbit of a dynamical system that passes through the point P and $\mathcal{O}^+(P)$ and $\mathcal{O}^-(P)$ will denote the positive and negative semi-orbit through P, respectively.

If E is an equilibrium point of a dynamical system, then $W^s(E)$ and $W^u(E)$ will denote the stable and unstable manifolds of E respectively.

2. The model — a food web

We shall consider the following model of predator-mediated competition in the chemostat:

$$\begin{aligned}
S'(t) &= (S^0 - S(t))D - \sum_{i=1}^{2} \frac{x_i(t)p_i(S(t))}{\eta_i},\\
x_1'(t) &= x_1(t)(-D + p_1(S(t))) - y(t)q(x_1(t))/z,\\
x_2'(t) &= x_2(t)(-D + p_2(S(t))), \qquad (2.1)\\
y'(t) &= y(t)(-D + q(x_1(t))),\\
S(0) = S_0 \geqslant 0, \quad & x_i(0) = x_{i0} \geqslant 0, \quad i = 1, 2, \quad y(0) = y_0 \geqslant 0.
\end{aligned}$$

In these equations $S(t)$ denotes the substrate concentration, $x_1(t)$ and $x_2(t)$ the concentrations of the competing populations and $y(t)$ the concentration of the predator population. $p_i(S)$ represents the per capita growth rate of the ith competitor, η_i is a growth yield constant, S^0 denotes the concentration of nutrient in the feed bottle and D denotes the input rate from the feed bottle and the washout rate from the growth chamber. In this model $x_1(t)$ is viewed as both a prey population and a competitor population. Here, $q(x_1)$ denotes the *per capita* growth rate of the predator population as a function of the prey concentration;

z is the growth yield factor for the predator population feeding on the prey; and we assume that $q(x_1)/z$ represents the prey-uptake function for the predator.

We make the following assumptions concerning the functions p_i and q in the model equations (2.1):

$$p_i, q: \mathbb{R}_+ \to \mathbb{R}_+; \tag{2.2}$$

$$p_i, q \text{ are continuously differentiable;} \tag{2.3}$$

$$p_1'(S) > 0 \quad \text{for all } S \in \mathbb{R}_+; \tag{2.4}$$

$$p_2'(S) \geqslant 0 \quad \text{for all } S \in \mathbb{R}_+; \tag{2.5}$$

$$q'(x_1) \geqslant 0 \quad \text{for all } x_1 \in \mathbb{R}_+; \tag{2.6}$$

$$p_i(0) = 0, \qquad q(0) = 0. \tag{2.7}$$

It will also be convenient to denote $q(x_1)$ as

$$q(x_1) = x_1 h(x_1). \tag{2.8}$$

Note that since q is (continuously) differentiable it follows that $\lim_{x \to 0} h(x) = q'(0)$ and so we define $h(0) = q'(0)$.

The system (2.1) describes a chemostat with nonreproducing substrate, constant input and dilution rate, perfect mixing in the growth vessel, insignificant death rates compared to dilution rate, and instantaneous adjustment of growth rates to changes in the concentration of nutrient. Furthermore, just as we assume that the substrate-uptake rate is proportional to the rate of conversion to competitor biomass, we assume that the prey-uptake rate is proportional to the rate of conversion to predator biomass. In this model two populations compete solely for an essential, growth-limiting substrate. Also a predator population predates on the competitor population that would be the sole survivor provided the predator population were absent.

This model is similar to the models studied by Jost et al. [23]. However in their model of a food web they allow the predator to predate on both competitors. In all of their models they use Michaelis–Menten kinetics to describe nutrient uptake and competitor (prey) growth. In the food chain that results when the second competitor is absent, they consider two different models, one with Michaelis–Menten kinetics describing predator–prey dynamics and the other with multiple saturation kinetics. Their experimental results seem to indicate that the latter model is more satisfactory. In the food web they derive a more complicated functional response for the predator that takes food preference into consideration but that reduces to multiple saturation dynamics when one competitor is absent.

Freedman and Waltman [15] consider a general Kolmogorov model of three interacting predator–prey populations. They derive persistence criteria for this general model and then illustrate their results in special cases. In particular, under certain conditions their system can be interpreted as two rival populations with a predator predating on either one or both of the rival populations.

May [27], Cramer and May [9] and Vance [43] show predator-mediated coexistence is possible in a model of a one predator-two prey community based on the "classical" Lotka–Volterra equations. Vance discovers a "quasi-cyclic" trajectory. Further analysis by Gilpin [18] indicates that this trajectory is an example of "continuous chaos." However, such complicated dynamics cannot automatically be assumed to occur in our model since our model is an example of the "resource-based" approach (see [45]) as opposed to the more general "classical" Kolmogorov type approach (see [13]). Restricted to competitive systems, the "resource-based" approach used in this paper predicts trivial dynamics (i.e. all trajectories asymptotically approach critical points) no matter the number of competitors (see [2, 5, 21]). On the other hand the "classical" models can give rise to almost any complicated dynamical behaviour for even three or four competitors (see Smale [39]).

The food chain that results when the second competitor is eliminated from the model (2.1) was studied by Butler, Hsu and Waltman [4], Bungay and Bungay [3] and Sell [37], among others. They all consider a model in which all functional responses are modelled by Michaelis-Menten type dynamics. Experiments [17] seem to show that this is quite reasonable for *soluble organic nutrient — heterotrophic bacteria — holozoic protozoa* food chains. Canale [7] considers M'Kendrick and Pai's [28] model (i.e. Lotka-Volterra dynamics). The food chain with very general dynamics is studied by Saunders and Bazin [36] and by Gard [16, 17].

3. The nondimensional version of the model

It will be more convenient to analyze the model after the following substitutions are performed:

$$\bar{t} = tD; \qquad \bar{S} = S/S^0; \qquad \bar{x}_i = x_i/\eta_i S^0; \qquad i = 1, 2; \qquad \bar{y} = y/S^0\eta_1 z. \tag{3.1}$$

$$\bar{p}_i(\bar{S}) = p_i(S)/D; \qquad i = 1, 2. \tag{3.2}$$

$$\bar{q}(\bar{x}_1) = q(x_1)/D \qquad (\text{and so } \bar{h}(\bar{x}_1) = \eta_1 S^0 h(x_1)/D). \tag{3.3}$$

Omitting the bars, in order to simplify the notation, the nondimensional version of model (2.1) can be written:

$$\begin{aligned}
S'(t) &= (1 - S(t)) - \sum_{i=1}^{2} x_i(t) p_i(S(t)),\\
x_1'(t) &= x_1(t)(-1 + p_1(S(t))) - y(t) q(x_1(t)),\\
x_2'(t) &= x_2(t)(-1 + p_2(S(t))),\\
y'(t) &= y(t)(-1 + q(x_1(t))),\\
S_0 &\geq 0, \qquad x_{i0} \geq 0, \qquad i = 1, 2, \qquad y_0 \geq 0.
\end{aligned} \tag{3.4}$$

All the Assumptions (2.2)-(2.8) hold for this nondimensional version of the system (2.1). Therefore, there will be no loss of generality if we study system (3.4) instead of (2.1) and we can always reinterpret our results in terms of the unscaled variables by the appropriate application of (3.1)-(3.3).

By the monotonicity assumptions (2.4)-(2.6) it follows that there exist uniquely defined positive extended real numbers λ_i and δ such that:

$$\begin{aligned}
p_i(S) &< 1 \quad \text{if } S < \lambda_i,\\
p_i(S) &> 1 \quad \text{if } S > \lambda_i,\\
q(x_1) &< 1 \quad \text{if } x_1 < \delta,
\end{aligned} \tag{3.5}$$

and

$$q(x_1) > 1 \quad \text{if } x_1 > \delta,$$

provided we make the following assumption of a generic nature:

$$\text{If } \lambda_2 \text{ (or } \delta\text{) is finite, then } p_2'(\lambda_2) > 0 \ (q'(\delta) > 0). \tag{3.6}$$

Assume also that

$$\text{all } \lambda_i, \delta \text{ (other than those which are infinite) are distinct from each other and from 1, and} \tag{3.7}$$

$$\lambda_1 < \lambda_2 \text{ if } \lambda_1 < \infty. \tag{3.8}$$

Then λ_i and δ represent the break-even concentrations of substrate and prey, respectively. Also in the absence of the predator, x_1 drives x_2 to extinction.

The critical points of the system (3.4) will be denoted:

$$E_1 = (1, 0, 0, 0)$$

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

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

$$E_{S^*} = (S^*, \delta, 0, y^*) \quad \text{where } y^* = \delta(-1 + p_1(S^*)) \text{ and } S^* \text{ satisfies } 1 - S^* = \delta p_1(S^*).$$

$$\hat{E}_{\lambda_2} = (\lambda_2, \delta, \hat{x}_2, \hat{y}) \quad \text{where } \hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2) \text{ and } \hat{y} = \delta(-1 + p_1(\lambda_2))$$

and will be assumed to be critical points if and only if all their components are nonnegative. Therefore E_{λ_1} (resp. E_{λ_2}) is a critical point provided $\lambda_1 \leq 1$ ($\lambda_2 \leq 1$) and $\hat{E}_{\lambda_2}$ is a critical point provided $\hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2) \geq 0$. In particular, this implies that $\lambda_2 + \delta < 1$. E_{S^*} is a critical point provided $S^* \geq 0$ is well-defined and $y^* \geq 0$. S^* is defined by the equation $1 - S^* = \delta p_1(S^*)$. If we plot the functions $1 - S$ and $\delta p_1(S)$ on the same graph, since $p_1(0) = 0$ and $p_1(S)$ strictly increases it follows that there is a unique point S^* that satisfies the equation $1 - S = \delta p_1(S)$ and this point lies between 0 and 1. In order for $y^* \geq 0$ we require $S^* \geq \lambda_1$. But the solution of $1 - S = \delta p_1(S)$ is less than λ_1 if and only if $1 - \lambda_1 < 1 - S = \delta p_1(S) < \delta p_1(\lambda_1) = \delta$, i.e. $1 - \lambda_1 < \delta$. Thus, E_{S^*} is a critical point provided that $\lambda_1 + \delta \leq 1$. Actually, since in this case $S^* \geq \lambda_1$, it follows that $1 - S^* = \delta p_1(S^*) \geq \delta$ and so when E_{S^*} is a critical point $\lambda_1 \leq S^* \leq 1 - \delta$.

4. Three-dimensional subsystems

In this section we briefly consider the three dimensional subsystems that result if one of the competitors or the predator is absent from the system.

If the predator is absent, i.e. $y_0 = 0$, then system (3.4) reduces to:

$$\begin{aligned} S'(t) &= (1 - S(t)) - \sum_{i=1}^{2} x_i(t) p_i(S(t)), \\ x_i'(t) &= x_i(t)(-1 + p_i(S(t))), \qquad i = 1, 2 \\ S_0 &\geq 0 \quad \text{and} \quad x_{i0} > 0, \qquad i = 1, 2. \end{aligned} \tag{4.1}$$

This is the basic chemostat model for two competing populations with arbitrary monotone uptake functions, and has been analyzed in [1, 5]. Competitor x_2 always dies out. In the following lemma, we paraphrase Corollary 3.5 from [5] as it applies to (4.1). Recall that $\lambda_1 < \lambda_2$.

Lemma 4.1. *If* $\lambda_1 > 1$, *the critical point* $(1, 0, 0)$ *is globally asymptotically stable for* (4.1). *If* $\lambda_1 < 1$, *the critical point* $(\lambda_1, 1-\lambda_1, 0)$ *is globally asymptotically stable for* (4.1).

If competitor x_1 is absent, i.e. $x_{10} = 0$, then (3.4) reduces to:

$$\begin{aligned} &S'(t) = (1 - S(t)) - x_2(t)p_2(S(t)), \\ &x_2'(t) = x_2(t)(-1 + p_2(S(t))), \\ &y'(t) = -y(t), \\ &S_0 \geq 0, \qquad x_{20} > 0 \quad \text{and} \quad y_0 > 0. \end{aligned} \tag{4.2}$$

Since the y equation decouples it is clear that $\lim_{t\to\infty} y(t) = 0$ and so asymptotically the model reduces to two dimensions consisting of S and x_2, only.

If competitor x_2 is absent then (3.4) has the form:

$$\begin{aligned} &S'(t) = (1 - S(t)) - x_1(t)p_1(S(t)), \\ &x_1'(t) = x_1(t)(-1 + p_1(S(t))) - y(t)q(x_1(t)), \\ &y'(t) = y(t)(-1 + q(x_1(t))), \\ &S_0 \geq 0, \qquad x_{10} \geq 0 \quad \text{and} \quad y_0 \geq 0. \end{aligned} \tag{4.3}$$

The critical points of this system will be denoted by: $E_1^3 = (1, 0, 0)$, $E_{\lambda_1}^3 = (\lambda_1, 1-\lambda_1, 0)$, and $E_{S^*}^3 = (S^*, \delta, y^*)$ where $y^* = \delta(-1 + p_1(S^*))$ and S^* satisfies $1 - S^* = \delta p_1(S^*)$ and will be considered critical points if and only if all the components are nonnegative.

System (4.3) describes a food chain where y eats x_1 which in turn eats S. It will be studied in more detail in Sect. 8 and the results of the linear analysis can be found in Appendix B.

For notational convenience we shall identify the nonnegative (S, x_1, y) cone with $\mathbb{R}_+^3$.

5. Preliminary results

The following lemmas are straightforward and similar to results given in [5] and [21].

Lemma 5.1. *All solutions* $S(t)$, $x_1(t)$, $x_2(t)$ *and* $y(t)$ *of* (3.4) *for which* $x_{i0} > 0$, $i = 1, 2$ *and* $y_0 > 0$ *are positive and bounded for* $t > 0$.

Lemma 5.2. *The simplex*

$$\mathscr{L} = \left\{ (S, x_1, x_2, y) \colon S, x_1, x_2, y \geq 0;\; S + \sum_{i=1}^{2} x_i + y = 1 \right\}$$

is a global attractor for (3.4).

It is evident that for all solutions of (3.4), $\underline{\lim}_{t\to\infty} S(t) > 0$.

It will be useful to consider the subsimplices $\mathscr{L}_H$ of $\mathscr{L}$:

$$\mathscr{L}_H = \{(S, x_1, x_2, y) \in \mathscr{L}: x_i = 0, i \neq H\} \tag{5.1}$$

where $H \subset \{1, 2\}$. Thus $\mathscr{L} = \mathscr{L}_{\{1,2\}}$.

The next result concerns extinction of a population due to insufficient nutrient. The extinction is independent of either competition or predation.

Lemma 5.3. *For all solutions of* (3.4):

(i) *if* $\lambda_i \geqslant 1$ *(or* $\lambda_i = +\infty$*), then* $\lim_{t\to\infty} x_i(t) = 0$;
(ii) *if* $\delta \geqslant 1$ *(or* $\delta = +\infty$*), then* $\lim_{t\to\infty} y(t) = 0$;
(iii) *if* $\lim_{t\to\infty} x_1(t) = 0$ *then* $\lim_{t\to\infty} y(t) = 0$.

6. Transfer of global stability

In this section we show that there is a hierarchy of critical points and that under certain conditions global stability transfers from one critical point to another as various parameters are decreased. In this instance, the global behaviour at each stage resides in a single equilibrium point.

Note that when $\lambda_1 > 1$, then E_1 is the only critical point in the nonnegative (S, x_1, x_2, y) cone, $\mathbb{R}^4_+$, and when $\lambda_1 = 1$, E_1 and E_{λ_1} coalesce. An immediate consequence of Lemmas 5.2 and 5.3 is

Lemma 6.1. *If* $\lambda_1 \geqslant 1$, *then* E_1 *is globally asymptotically stable for* (3.4).

Now we shall maintain $\lambda_1 + \delta > 1$, but allow λ_1 to decrease below 1. We shall show that as E_{λ_1} appears in $\mathbb{R}^4_+$ there is a transfer of global stability from E_1 to E_{λ_1}, and E_{λ_1} remains globally asymptotically stable provided $1 - \delta < \lambda_1 < 1$. In this parameter range E_1, E_{λ_1}, and if $\lambda_2 \leqslant 1$, E_{λ_2}, are the only equilibria in $\mathbb{R}^4_+$. In order to prove this we shall use the following lemma, whose proof is straightforward and omitted.

Lemma 6.2. *Assume* $\lambda_1 < 1$. *Then for any solution of* (3.4) *for which* $x_{10} > 0$, $\overline{\lim}_{t\to\infty} x_1(t) > 0$.

Theorem 6.3. *If* $1 - \delta < \lambda_1 < 1$, *then* E_{λ_1} *is globally asymptotically stable for* (3.4) *with respect to all solutions with initial conditions satisfying* $x_{10} > 0$.

Proof. Let $(S(t), x_1(t), x_2(t), y(t))$ be a solution of (3.4) and let Ω denote its omega-limit set. Since $1 - \delta < \lambda_1 < 1$, E_{λ_1} is locally asymptotically stable for (3.4) (see Appendix A). Therefore $E_{\lambda_1} \in \Omega$ implies $\Omega = \{E_{\lambda_1}\}$. By Lemma 6.2, $\overline{\lim}_{t\to\infty} x_1(t) > 0$, and so there exists $P = (\bar{S}, \bar{x}_1, \bar{x}_2, \bar{y}) \in \Omega$ with $\bar{x}_1 > 0$. Let $\bar{\gamma}(t) = (\bar{S}(t), \bar{x}_1(t), \bar{x}_2(t), \bar{y}(t))$, where $\bar{\gamma}(0) = P$, be the solution of (3.4) through P and denote its orbit by $\mathcal{O}(P)$. Since $\operatorname{cl} \mathcal{O}(P) \subset \Omega$, if $\bar{y} = 0$ then $E_{\lambda_1} \in \Omega$ by Lemma 4.1. If $\bar{y} \neq 0$, by the preceding argument it suffices to show that $\lim_{t\to\infty} \bar{y}(t) = 0$.

Assume $\delta < 1$ or the result follows by Lemma 5.3(ii). Define ε such that $1 - \delta + \varepsilon = \lambda_1$. Then $\varepsilon > 0$. Since $P \in \Omega$ and $\Omega \subset \mathscr{L}$ by Lemma 5.2,

$$(\bar{S} + \bar{x}_1 + \bar{x}_2 + \bar{y})(t) = 1 \quad \text{for all } t \geqslant 0, \tag{6.1}$$

and

$$(\bar{S} + \bar{x}_1 + \bar{x}_2 + \bar{y})'(t) = 0 \quad \text{for all } t \geqslant 0. \tag{6.2}$$

If $\overline{\lim}_{t\to\infty} \bar{S}(t) < \lambda_1$, then $\lim_{t\to\infty} \bar{x}_1(t) = 0$ contradicting Lemma 6.2. But $\overline{\lim}_{t\to\infty} \bar{S}(t) \geq \lambda_1$ implies that $\bar{S}(t) > \lambda_1$ for all large t or there exists $\tau \geq 0$ such that $\lambda_1 \geq \bar{S}(\tau) \geq \lambda_1 - \varepsilon/2$. By (6.1) $\bar{x}_1(\tau) \leq 1 - \bar{S}(\tau) \leq 1 - (\lambda_1 - \varepsilon/2) = \delta - \varepsilon/2$. But then $\bar{y}'(\tau) \leq \bar{y}(\tau)(-1 + q(\delta - \varepsilon/2)) < 0$. $\bar{S}(\tau) \leq \lambda_1$ implies $\bar{x}_1'(\tau) \leq 0$ and $\bar{x}_2'(\tau) \leq 0$. Therefore, by (6.2) $\bar{S}'(\tau) > 0$ and so $\bar{S}(\tau) \geq \lambda_1 - \varepsilon/2$ for all $t \geq \tau$. In any case it follows that $\bar{S}(t) \geq \lambda_1 - \varepsilon/2$ for all sufficiently large t and so $\bar{x}_1(t) \leq \delta - \varepsilon/2$ for all large t. This implies $\lim_{t\to\infty} \bar{y}(t) = 0$. The result follows. □

Next we shall assume that λ_2 is sufficiently large so that $\hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2) < 0$. This is equivalent to $S^* \leq \lambda_2$. However, we shall allow the sum $\lambda_1 + \delta$ to decrease. When $\lambda_1 + \delta = 1$ then E_{λ_1} and E_{S^*} coalesce, i.e. $S^* = \lambda_1$ and $y^* = 0$. Therefore condition (A.2) (i.e. $y^*(\delta q'(\delta) - 1)/\delta + \delta p_1'(S^*) > 0$) holds, since $p_1'(\lambda_1) > 0$ by (2.4). By the continuity of the roots of the characteristic equation as a function of its coefficients, it follows that as the sum $\lambda_1 + \delta$ decreases below 1, E_{S^*} is at least initially locally asymptotically stable (see Appendix A). At the same time E_{λ_1} loses not only its global stability but also its local stability since $1 - \lambda_1 > \delta$ implies that the eigenvalue $-1 + q(1 - \lambda_1)$ is positive (see Appendix A).

Thus far our discussion has been for the general system (3.4). In certain special cases E_{S^*} picks up the global stability lost by E_{λ_1} and maintains it provided $\lambda_1 + \delta < 1$ and $1 - \lambda_2 - \delta p_1(\lambda_2) < 0$. In this case, if we allow λ_2 and/or δ to decrease, once $1 - \lambda_2 - \delta p_1(\lambda_2) = 0$, E_{S^*} and $\hat{E}_{\lambda_2}$ coalesce. As these parameters decrease further, E_{S^*} loses its local stability since then $S^* > \lambda_2$, and there is a transfer of global stability to $\hat{E}_{\lambda_2}$. The transition from competitive exclusion to persistence is complete and the global attractor at each stage is a single equilibrium point. That this nice sequential transfer of global stability from one critical point to another is not always the case with general monotone kinetics will be demonstrated by an example in Sect. 9.

The global stability results that follow can be obtained through Lyapunov function arguments. The details are given in [46].

Theorem 6.4. *Assume that* $\lambda_1 + \delta < 1$. *If* $x_{20} > 0$, *assume that* $1 - \lambda_2 - \delta p_1(\lambda_2) < 0$. *Let* $q(x_1)$ *be linear, i.e.* $q(x_1) = x_1/\delta$ *and assume that each* $p_i(S)$, $i = 1, 2$ *is either linear, i.e.* $p_i(S) = S/\lambda_i$ *or Michaelis-Menten, i.e.* $p_i(S) = m_i S/(\lambda_i(m_i - 1) + S)$. *Then* E_{S^*} *is globally asymptotically stable for* (3.4) *with respect to all solutions for which* $x_{10} > 0$ *and* $y_0 > 0$.

Theorem 6.5. *Assume that* $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$. *Let* $q(x_1) = x_1/\delta$ *and assume that for each* $i = 1, 2$ *either* $p_i(S) = S/\lambda_i$ *or* $p_i(S) = m_i S/(\lambda_i(m_i - 1) + S)$. *Then* $\hat{E}_{\lambda_2}$ *is globally asymptotically stable with respect to solutions of* (3.4) *for which* $x_{i0} > 0$, $i = 1, 2$ *and* $y_0 > 0$. (*Recall that* $\hat{E}_{\lambda_2} = (\lambda_2, \delta, \hat{x}_2, \hat{y})$ *where* $\hat{x}_2 = 1 - \lambda_2 - \delta p_1(\lambda_2)$ *and* $\hat{y} = \delta(-1 + p_1(\lambda_2))$.)

Theorems 6.4 and 6.5 indicate that the evolution of the global attractor for the system (as various parameters are varied, making conditions favourable enough for a new population to survive) takes a very simple form if the appropriate assumptions of Lotka-Volterra or Michaelis-Menten kinetics are made.

7. A simple food chain

We first encountered the following food chain in Sect. 4 (see system (4.3)) where we considered the three dimensional subsystems of the food web (3.4).

$$\begin{aligned} S'(t) &= 1 - S(t) - x(t)p(S(t)), \\ x'(t) &= x(t)(-1 + p(S(t))) - y(t)q(x(t)), \\ y'(t) &= y(t)(-1 + q(x(t))), \\ & S_0, x_0, \text{and } y_0 \geqslant 0. \end{aligned} \tag{7.1}$$

We drop the subscript 1 here (except for λ_1), since there is no ambiguity, and we use the notation for the critical points (E_1^3, $E_{\lambda_1}^3$, and $E_{S^*}^3$) introduced for system (4.3).

System (7.1) has been studied by others (e.g. [4, 12, 17, 24, 37, 42]). Except for Butler et al. [4] and Gard [17] most of the previous work has concerned local stability analysis, numerical solutions or experimental results. The local analysis is summarized in Appendix B.

Note that all the results in Sects. 5 and 6 apply to (7.1) with the obvious modifications. In particular, there is a transference of global stability from E_1^3 to $E_{\lambda_1}^3$ as λ_1 decreases below 1 and at least a transference of local stability from $E_{\lambda_1}^3$ to $E_{S^*}^3$ as $\lambda_1 + \delta$ decreases below 1.

In the special case that the functional response q is Lotka-Volterra and p satisfies either Lotka-Volterra or Michaelis-Menten kinetics, by Corollary 6.6, $E_{S^*}^3$ is globally asymptotically stable provided $\lambda_1 + \delta < 1$.

Assuming the functional responses p and q both satisfy Michaelis-Menten kinetics, Butler et al. [4] use the Poincaré criterion (see, e.g. Coppel [8]) to show that $E_{S^*}^3$ is globally asymptotically stable whenever it is locally asymptotically stable. Since $E_{S^*}^3$ is at least initially asymptotically stable as $\lambda_1 + \delta$ decreases below 1, this implies that in this case, there is a transfer of global stability from $E_{\lambda_1}^3$ to $E_{S^*}^3$. They also show that if $E_{S^*}^3$ is ever unstable then there is at least one periodic orbit surrounding it. They conjecture that if $E_{S^*}^3$ is unstable then the limit cycle is unique and hence must be a global attractor with respect to noncritical orbits with positive initial conditions. Though they do not comment, by their method of proof they actually show that if $E_{S^*}^3$ loses stability by decreasing $\lambda_1 + \delta$ appropriately, then a certain inequality (see Appendix (B1) must be reversed and so at least initially there is a unique periodic orbit which is globally attracting with respect to noncritical orbits with positive initial conditions. In this case, then, there is a transfer of global stability from $E_{S^*}^3$ to a bifurcating periodic orbit (as $\lambda_1 + \delta$ decreases).

Gard [17] on the other hand, considers a more general model than (7.1) which reduces to (7.1) if the function $g(x)$ in his model is taken to be $1 - x$ and the parameters a, b, c and d in his model are all equal to 1. In this case Gard obtains conditions under which weak persistence occurs (see Definition 1.1). He also shows that there is a unique interior equilibrium and if the equilibrium is unstable there is a nontrivial periodic orbit with trajectory in $L_{\{1\}} \cap \mathbb{R}_+^3$.

In this section we show that (7.1) is persistent using a technique similar to the one used to prove Theorem 2.1 in [15]. This strengthens a result of Gard [17] in which just weak persistence was obtained. We also prove several results which will be used in Sect. 8 to show uniform persistence of (3.4). These results are interesting in themselves since they concern the eventual behaviour of solutions of (7.1).

Theorem 7.1. *Let* $\gamma(t)=(S(t), x(t), y(t))$ *be a solution of* (7.1). *Then*

(i) $\underline{\lim}_{t\to\infty} S(t)>0$.
(ii) *if* $\lambda_1<1$ *and* $x_0>0$, $\underline{\lim}_{t\to\infty} x(t)>0$.
(iii) *if* $\lambda_1+\delta<1$ *and* x_0, $y_0>0$, $\underline{\lim}_{t\to\infty} y(t)>0$, *thus* (7.1) *is persistent.*

Proof: (i) is obvious.

(ii) Let Ω denote the omega-limit set of $\gamma(t)$. By Theorem 5.1 $\Omega\subset\mathbb{R}^3_+$ is compact.

Assume $\lambda_1<1$ and $x_0>0$. Suppose $E_1^3\in\Omega$. Since $\lambda_1<1$, E_1^3 is an unstable hyperbolic critical point (see Appendix B) with stable manifold $W^s(E_1^3)=\{(S,x,y)\colon S\geq 0, x=0, y\geq 0\}$. Since $\gamma(0)\notin W^s(E_1)$, $\Omega\neq\{E_1^3\}$. By Lemma 5.2 of [5] (see also [15]), there exists $P^s\in(W^s(E_1^3)\backslash\{E_1^3\})\cap\Omega$. By Lemma 5.2, $P^s\in\Omega\subset\mathcal{L}_{\{1\}}$, a positively invariant set. But then $\mathcal{O}^-(P^s)\not\subset\mathbb{R}^3_+$, a contradiction since $P^s\in\Omega$ implies that $\mathrm{cl}(\mathcal{O}(P^s))\subset\Omega\subset\mathbb{R}^3_+$. Therefore $E_1^3\notin\Omega$.

Suppose $\lambda_1<1$, $x_0>0$ and $\underline{\lim}_{t\to\infty} x(t)=0$. Then there exists $P=(\bar{S},0,\bar{y})\in\Omega$ and so $\mathrm{cl}(\mathcal{O}(P))\subset\Omega$. By Lemma 5.3(iii), $E_1^3\in\Omega$, a contradiction. Therefore $\underline{\lim}_{t\to\infty} x(t)>0$.

(iii) Suppose $\lambda_1+\delta<1$, x_0, $y_0>0$. By a similar argument to the one used above to show $E_1^3\notin\Omega$, it can be shown that $E_{\lambda_1}^3\notin\Omega$. Assume $\underline{\lim}_{t\to\infty} y(t)=0$. Then there exists $Q=(\tilde{S},\tilde{x},0)\in\Omega$ where $\tilde{x}>0$ since $\underline{\lim}_{t\to\infty} x(t)>0$ by (ii). It follows from Lemma 4.1 that $E_{\lambda_1}^3\in\mathrm{cl}(\mathcal{O}(Q))\subset\Omega$, a contradiction. Therefore $\underline{\lim}_{t\to\infty} y(t)>0$. □

Remark 7.2: In Theorem 7.1(iii), we can in fact prove the stronger assertion of uniform persistence by using the results of [6]. The main result of [6], paraphrased in our context, asserts that if $\mathcal{F}$ is a dynamical system for which $\mathbb{R}^n_+$ and its boundary are invariant, then $\mathcal{F}$ is uniformly persistent provided the following conditions hold:

(1) $\mathcal{F}$ is dissipative
(2) $\mathcal{F}$ is weakly persistent
(3) $\partial\mathcal{F}$ (the restriction of $\mathcal{F}$ to the boundary of $\mathbb{R}^n_+$) is "isolated"
(4) $\partial\mathcal{F}$ is "acyclic."

Although the dynamical system defined by (7.1) is not invariant on $\mathbb{R}^3_+$ or its boundary, the result quoted above is easily modified to apply to a dynamical system $\mathcal{F}$ on $\mathbb{R}^n_+$ for which the boundary $\partial\mathbb{R}^n_+$ is the union of two sets B_1 and B_2 such that B_1 is invariant under $\mathcal{F}$ and B_2 is a "repeller" into the interior of $\mathbb{R}^n_+$, provided that conditions (3) and (4) above are satisfied by $\partial\mathcal{F}_1$, the restriction of $\mathcal{F}$ to B_1.

For the system (7.1), condition (1) above holds by Theorem 5.2, and a stronger statement than condition (2) above has just been proved in Theorem 7.1(iii). Conditions (3) and (4) are somewhat technical to describe in general, but roughly speaking they are satisfied if the invariant sets on $\partial\mathbb{R}^n_+$ "repel" into the interior of $\mathbb{R}^n_+$ and are not "cyclically linked" by solution trajectories lying in $\partial\mathbb{R}^n_+$.

In the case of Theorem 7.1(iii), (3) and (4) hold, for the (x,y)-face of $\partial\mathbb{R}^3_+$ "repels" into the interior of $\mathbb{R}^3_+$ and the only invariant sets in $\partial\mathbb{R}^3_+$ are the critical points E_1^3 and $E_{\lambda_1}^3$. Thus we have uniform persistence. This also implies that (7.1) has a compact weak global attractor lying in the interior of $\mathbb{R}^3_+$ [6].

We have therefore shown that no matter how tenacious the predator, provided the substrate concentration is sufficient for the prey to survive in pure competition, it will survive predation in the sense that its concentration remains bounded away from zero for all positive time. To avoid extinction of the predator, however, the predator must be efficient enough, i.e. $\lambda_1+\delta<1$. In this case the food chain persists. On the other hand it is possible to show that the more efficient the predator (i.e. the closer δ is to zero), the smaller the prey concentration is "*on the average*" and even though the prey concentration is bounded away from zero, the closer that bound is to zero. This is basically the content of the next lemma in which we clarify what we mean by "*on the average.*" We shall also require this lemma and the following as technical lemmas for our discussion of persistence of the food web in Sect. 8. However, before stating the next lemma we introduce the following parametrization of (7.1):

$$\begin{aligned} S'(t)&=1-S(t)-x(t)p(S(t)),\\ x'(t)&=x(t)(-1+p(S(t)))-y(t)q_\delta(x(t)),\\ y'(t)&=y(t)(-1+q_\delta(x(t))),\\ &S_0,\, x_0 \text{ and } y_0\geq 0. \end{aligned} \tag{7.2$_\delta$}$$

We assume that the function q_δ satisfies all the usual assumptions on q (i.e. (2.2)-(2.3); (2.6)-(2.8); and (3.5)-(3.7)). In addition we assume that

$$\lim_{\delta\to0^+} q_\delta(\varepsilon)=+\infty \quad \text{for every fixed } \varepsilon>0. \tag{7.3}$$

It may be verified that if q satisfies Lotka-Volterra, Michaelis-Menten or multiple saturation kinetics then q can be parametrized in this way. In these examples $\delta\to0^+$ is equivalent to the maximum growth rate tending to $+\infty$.

Lemma 7.3. *Let $\varepsilon>0$ be given. Assume that $\lambda_1+\delta<1$. Let $(S(t), x(t), y(t))$ be any fixed solution of (7.2)$_\delta$ for which $x_0>0$ and $y_0>0$. Choose $l>0$, $L>1$ and $\bar{T}\geq 0$ such that $l<y(t)<L$ for all $t\geq\bar{T}$ where l and $\bar{T}$ depend on δ and the solution. (This is possible by Lemmas 5.1, 5.2 and Theorem 7.1.) Select any $T>\ln(L/l)$ and any $s\geq T+\bar{T}$. Define $A=\{t\in[s-T, s]: x(s)\geq\varepsilon\}$, $a=\mu(A)$, the Lebesgue measure of A, and $\alpha=(1/T)\mu(A)$. Then $\alpha<2/q_\delta(\varepsilon)$.*

Proof: Define A^c to be $[s-T, s]\backslash A$.

$$\text{If } t\in A \text{ then } y'(t)/y(t)\geq -1+q_\delta(\varepsilon).$$

$$\text{If } t\in A^c \text{ then } y'(t)/y(t)\geq -1.$$

Integrating the y equation from $s-T$ to s yields:

$$\begin{aligned} \ln(y(s)/y(s-T))&\geq\int_A(-1+q_\delta(\varepsilon))\,d\mu+\int_{A^c}-1\,d\mu\\ &=(-1+q_\delta(\varepsilon))a-(T-a)\\ &=T(\alpha q_\delta(\varepsilon)-1). \end{aligned}$$

Therefore $\alpha < 2/q_\delta(\varepsilon)$ since otherwise

$$\ln(L/l) \geq \ln(y(s)/y(s-T)) \geq T,$$

a contradiction. □

We can also show that if $\delta > 0$ is sufficiently small then "*on the average*" the S-component of any solution eventually remains close to one. This is made rigorous in the following lemma.

Lemma 7.4. *Choose* ε *such that* $0<\varepsilon<1/4$ *and choose* $L>1$. *Let* $M=\max(L, p(L))$. *Assume* $\delta>0$ *is sufficiently small so that* $\lambda_1+\delta<1$ *and* $q_\delta(\varepsilon)>4(1+M/\varepsilon k)/\sqrt{\varepsilon}$, *where* $k=(1/\sqrt{\varepsilon})-1$. *Let* $(S(t), x(t), y(t))$ *be any fixed solution of* $(7.2)_\delta$ *for which* $x_0>0$ *and* $y_0>0$. *Choose* $l>0$ *and* $\bar{T}>0$ *so that*

$$l \leq y(t) \leq L, \qquad 0 \leq S(t) \leq L, \quad \textit{and} \quad 0 \leq x(t) \leq L$$

for all $t \geq \bar{T}$. *Select*

$$T > \max(\ln(L \backslash l), 2/\varepsilon, \bar{T})$$

such that

$$S(t) < 1 + \varepsilon M \quad \textit{for all } t \geq T.$$

For any $s \geq 2T$, *define*

$$B = \{t \in [s-T, s]: S(t) \leq 1-(1+k)\varepsilon M\}$$

$$b = \mu(B) \quad \textit{and} \quad \beta = \frac{1}{T}\mu(B).$$

Then $\beta < 6\sqrt{\varepsilon}$.

Proof. Define

$$A = \{t \in [s-T, s]: x(t) \geq \varepsilon\},$$

$$a = \mu(A) \quad \text{and} \quad \alpha = \frac{1}{T}\mu(A).$$

Let B^c denote $[s-T; s]\backslash B$. Then $[s-T, s] = \bigcup_{i=1}^4 G_i$ where

$$G_1 = B \cap A^c \quad (\text{and so } \mu(G_1) \geq b-a),$$
$$G_2 = B \cap A \quad (\text{and so } \mu(G_2) \leq a),$$
$$G_3 = B^c \cap A^c \quad (\text{and so } \mu(G_3) \leq T),$$
$$G_4 = B^c \cap A \quad (\text{and so } \mu(G_4) \leq a).$$

Then,

$$S'(t) \geq 1-(1-(1+k)\varepsilon M)-\varepsilon M = \varepsilon k M \quad \text{for } t \in G_1,$$
$$S'(t) \geq 1-(1-(1+k)\varepsilon M)-M^2 \geq -M^2 \quad \text{for } t \in G_2,$$
$$S'(t) \geq 1-(1+\varepsilon M)-\varepsilon M \geq -2\varepsilon M \qquad \text{for } t \in G_3,$$

and

$$S'(t) \geqslant 1-(1+\varepsilon M)-M^2 = -\varepsilon M - M^2 \quad \text{for } t \in G_4,$$

since s is chosen sufficiently large.

Integrating the S equation from $s-T$ to s yields

$$M \geqslant S(s)-S(s-T) \geqslant \varepsilon k M(b-a) - M^2 a - 2\varepsilon M T - (\varepsilon M + M^2)a.$$

Therefore,

$$b \leqslant a(1+1/k) + (1+2Ma+2\varepsilon T)/\varepsilon k,$$

or

$$\beta \leqslant 2\alpha + 1/T\varepsilon k + 2M\alpha/\varepsilon k + 2/k,$$

since $k > 1$ if $0 < \varepsilon < 1/4$

$$\leqslant 6\sqrt{\varepsilon}$$

since $T > 2/\varepsilon$ by selection, and for $0 < \varepsilon < 1/4$, $k > 1/(2\sqrt{\varepsilon})$ which implies that $1/T\varepsilon k < \sqrt{\varepsilon}$ and $2/k < 4\sqrt{\varepsilon}$. Also, $2\alpha(1+M/\varepsilon k) < \sqrt{\varepsilon}$ by Lemma 7.3 since $q_\delta(\varepsilon) > 4(1+M/\varepsilon k)/\sqrt{\varepsilon}$. ☐

Since by Lemma 5.2, $S+x+y \to 1$, it is evident that if the hypothesis of the preceding Lemma hold then "*on the average*" the y-component of any solution eventually remains close to zero provided $\delta > 0$ is sufficiently small.

8. Persistence of the food web

In this section, we again focus our attention on the food web described by model (3.4), and obtain conditions under which system (3.4) uniformly persists.

We begin with the results that require the fewest restrictions on the functions p_i, $i=1, 2$ and q. If not otherwise stated, the only assumptions on these functions are those given in Sects. 2 and 3.

Lemma 8.1. *For any solution of* (3.4):

(i) *if* $\lambda_1 < 1$ *and* $x_{10} > 0$, *then* $\underline{\lim}_{t\to\infty} x_1(t) > 0$;

(ii) *if* $\lambda_1 + \delta < 1$ *and* x_{10}, $y_0 > 0$, *then* $\underline{\lim}_{t\to\infty} y(t) > 0$.

Proof. Let $\gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ be a solution of (3.4) and let Ω denote the omega-limit set of $\gamma(t)$.

(i) Assume $\lambda_1 < 1$ and $x_{10} > 0$. Suppose $\underline{\lim}_{t\to\infty} x_1(t) = 0$. Then there exists $\bar{P} = (\bar{S}, 0, \bar{x}_2, \bar{y}) \in \Omega$, and by Lemma 5.2, $\bar{S}+\bar{x}_2+\bar{y} = 1$. By Lemma 5.1, Ω is compact and contained in $\mathbb{R}^4_+$. From (4.2) it follows that

$$\text{at least one of } E_1 \text{ or } E_{\lambda_2} \text{ (if } \lambda_2 < 1) \in \Omega \tag{8.1}$$

Suppose $E_1 \in \Omega$. $\Omega \neq \{E_1\}$ since by Lemma 6.2, $\overline{\lim}_{t\to\infty} x_1(t) > 0$. Since E_1 is hyperbolic (see Appendix A), by Lemma 5.2 of [5], there exists $P^s \in (W^s(E_1)\backslash\{E_1\}) \cap \Omega$. But $W^s(E_1) = \{(S, x_1, x_2, y) \in \mathbb{R}^4_+ : x_1 = 0 \text{ and if } \lambda_2 < 1 \text{ then } x_2 = 0\}$. Thus $P^s \in \{(S, x_1, x_2, y) \in \mathscr{L}: x_1 = 0,\ y \geqslant 0 \text{ and if } \lambda_2 < 1 \text{ then } x_2 = 0\}$. If $\lambda_2 \geqslant 1$, by Lemma 5.3(i), $\lim_{t\to\infty} x_2(t) = 0$ and so there is no loss of generality if we assume $\lambda_2 < 1$. But then $\mathcal{O}^-(P^s) \not\subset \mathbb{R}^4_+$. Since $P^s \in \Omega$ implies that $\mathrm{cl}(\mathcal{O}(P^s)) \subset \Omega$, we have derived a contradiction. Therefore $E_1 \notin \Omega$. Suppose $\lambda_2 < 1$ and $E_{\lambda_2} \in \Omega$. $\{E_{\lambda_2}\} \neq \Omega$ since $\overline{\lim}_{t\to\infty} x_1(t) > 0$. Since E_{λ_2} is hyperbolic, by Lemma 5.2 of [5], there exists $Q^s \in (W^s(E_{\lambda_2}) \backslash \{E_{\lambda_2}\}) \cap \Omega$. Since $W^s(E_{\lambda_2}) = \{(S, x_1, x_2, y) \in \mathbb{R}^4_+ \colon x_1 = 0, x_2 > 0\}$ and $\Omega \subset \mathcal{L}$, $Q^s \in \{(S, x_1, x_2, y) \in \mathcal{L} \colon x_1 = 0, x_2 > 0\}$, a two-dimensional positively invariant set. By the Poincaré-Bendixson Theorem, either $E_1 \in \Omega$ or $\mathcal{O}^-(Q^s) \not\subset \mathbb{R}^4_+$. But both alternatives are impossible. Therefore $E_{\lambda_2} \notin \Omega$. Hence, by (8.1) $\underline{\lim}_{t\to\infty} x_1(t) > 0$.

(ii) Assume $\lambda_1 + \delta < 1$ and x_{10}, $y_0 > 0$. Suppose $\lim_{t\to\infty} y(t) = 0$. Then the system reduces to the chemostat model (4.1). Since $x_{10} > 0$, $\lim_{t\to\infty} S(t) = \lambda_1$, $\lim_{t\to\infty} x_1(t) = 1 - \lambda_1$ and $\lim_{t\to\infty} x_2(t) = 0$ by Lemma 4.1. But $1 - \lambda_1 > \delta$ and so, since $y_0 > 0$, $y'(t) > 0$ for all sufficiently large t. Therefore

$$\lim_{t\to\infty} y(t) \neq 0. \tag{8.2}$$

If $\lambda_2 \geq 1$, by Theorem 5.3(i), $\lim_{t\to\infty} x_2(t) = 0$ and so the result follows by Theorem 7.1. Therefore, assume $\lambda_2 < 1$. Suppose $\underline{\lim}_{t\to\infty} y(t) = 0$. Then there exists $\bar{P} = (\bar{S}, \bar{x}_1, \bar{x}_2, 0) \in \Omega$ with $\bar{S} + \bar{x}_1 + \bar{x}_2 = 1$. $\bar{P} \in \Omega$ implies that cl $\mathcal{O}(\bar{P}) \subset \Omega$ and so at least one of E_1, E_{λ_1} or $E_{\lambda_2} \in \Omega$. But by part (i), $\underline{\lim}_{t\to\infty} x_1(t) > 0$ and so $E_1 \notin \Omega$ and $E_{\lambda_2} \notin \Omega$. Suppose $E_{\lambda_1} \in \Omega$. By (8.2) $\lim_{t\to\infty} y(t) \neq 0$. Therefore $\{E_{\lambda_1}\} \neq \Omega$. Since E_{λ_1} is hyperbolic (see Appendix A), by Lemma 5.2 of [5], there exists $P^s \in (W^s(E_{\lambda_1}) \backslash \{E_{\lambda_1}\}) \cap \Omega$ where $W^s(E_{\lambda_1}) = \{(S, x_1, x_2, y) \in \mathbb{R}^4_+ \colon x_1 > 0, y = 0\}$. Since $P^s \in \Omega \subset \mathcal{L}$, $P^s \in \{(S, x_1, x_2, y) \in \mathcal{L} \colon x_1 > 0, y = 0\}$. Now either E_1 or $E_{\lambda_2} \in \mathrm{cl}\,\mathcal{O}^-(P^s)$ or cl $\mathcal{O}^-(P^s) \not\subset \mathbb{R}^4_+$. None of these alternatives is possible. Hence $\underline{\lim}_{t\to\infty} y(t) > 0$. ☐

Part (i) of this lemma tells us that if the system is viewed purely deterministically, the introduction of a predator cannot reverse the outcome of the competition. We comment further on this in the discussion in Sect. 10.

It is evident from Lemma 6.1 and Theorem 6.3 that a necessary condition for persistence of (3.4) is that $\lambda_1 + \delta < 1$. This condition is certainly not sufficient since E_{S^*} is locally asymptotically stable if, as well, $\lambda_1 + \delta$ is sufficiently close to 1. The next few results deal with sufficient conditions for persistence of (3.4).

The proof of the following Lemma is similar to the proof of Theorem 7.1.

Lemma 8.2. *Let* $\gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ *be any solution of* (3.4) *such that* $x_{i0} > 0$ $i = 1, 2$, $y_0 > 0$ *and* $\underline{\lim}_{t\to\infty} x_2(t) > 0$. *Then* $\underline{\lim}_{t\to\infty} S(t) > 0$, $\underline{\lim}_{t\to\infty} x_1(t) > 0$ *and* $\underline{\lim}_{t\to\infty} y(t) > 0$.

Theorem 8.3. *Assume* $\lambda_2 < 1$. *Assume also that* $q(x(t)) = q_\delta(x(t))$ *where* $\lim_{\delta\to 0^+} q_\delta(\varepsilon) = +\infty$ *for any fixed* $\varepsilon > 0$. *Provided* $\delta > 0$ *is sufficiently close to zero, it follows that* $\underline{\lim}_{t\to\infty} x_2(t) > 0$ *for any solution of* (3.4) *for which* $S_0 \geq 0$, x_{i0}, $y_0 > 0$ $i = 1, 2$ *and hence system* (3.4) *is persistent.*

Proof. Define

$$\bar{\varepsilon} = p_2(\lambda_2 + (1 - \lambda_2)/2) - 1. \tag{8.4}$$

Then $\bar{\varepsilon} > 0$ since $\lambda_2 < 1$. Choose $L > 1$ and let $M = \max(L, p(L))$. Select $\varepsilon > 0$ such that

$$\varepsilon < \min\left[\frac{1}{4}, \left(\frac{1 - \lambda_2}{4M}\right)^2, \left(\frac{\bar{\varepsilon}}{6(1 + \bar{\varepsilon})}\right)^2\right]. \tag{8.5}$$

Choose $\delta > 0$ sufficiently small so that

$$\lambda_1 + \delta < 1 \quad \text{and} \quad q_\delta(\varepsilon) > 4(1 + M/\varepsilon k)/\sqrt{\varepsilon}, \quad \text{where } k = (1/\sqrt{\varepsilon}) - 1. \tag{8.6}$$

Let $\gamma(t) = (S(t), x_1(t), x_2(t), y(t))$ be a fixed solution of (3.4) for which $S_0 \geqslant 0$ and x_{i0}, $y_0 > 0$ $i = 1, 2$. Assume $\underline{\lim}_{t\to\infty} x_2(t) = 0$. Then, there exists a sequence $\{t_n\}$ with $t_n \to \infty$ as $n \to \infty$ such that $x_2(t_n) \to 0$ and $x_2(t_n) < x_2(t)$ for all $t < t_n$. Since all solutions are bounded, without loss of generality, we assume that $\gamma(t_n) \to \bar{P} = (\bar{S}, \bar{x}_1, 0, \bar{y})$ (passing to a subsequence and relabelling if necessary). Let $\bar{\gamma}(t) = (\bar{S}(t), \bar{x}_1(t), 0, \bar{y}(t))$ denote the solution of (3.4) through $\bar{P}$. Since $\lambda_1 + \delta < 1$, by Lemma 8.1, $\bar{x}_1(0) > 0$ and $\bar{y}(0) > 0$.

Choose $l > 0$ and $\bar{T} \geqslant 0$ with respect to the solution $\bar{\gamma}(t)$ so that

$$l \leqslant \bar{y}(t) \leqslant L,$$

$$0 \leqslant \bar{S}(t) \leqslant L, \quad \text{and}$$

$$0 \leqslant \bar{x}(t) \leqslant L$$

for all $t \geqslant \bar{T}$. Select

$$T > \max[2/\varepsilon, \ln(L/l), \bar{T}], \tag{8.7}$$

such that

$$\bar{S}(t) < 1 + \varepsilon M \quad \text{for all } t \geqslant T.$$

Since the functions on the right-hand side of (3.4) are C^1 and since (3.4) is autonomous with all solutions bounded, it follows by continuous dependence on initial conditions that there exists $\bar{\delta} > 0$ such that $\rho(\gamma(\tau), \bar{\gamma}(\tau)) < \bar{\delta}$ implies that $\rho(\gamma(t), \bar{\gamma}(t)) < \sqrt{\varepsilon} M$ for all $t \in [\tau - T, \tau]$ where $\bar{\delta}$ depends on T but not on τ. Here the metric ρ is defined by $\rho(a, b) = \sum_{i=1}^{4} |a_i - b_i|$ if $a = (a_1, a_2, a_3, a_4)$ and $b = (b_1, b_2, b_3, b_4)$. Since $\gamma(t_n) \to \bar{P}$, there exists $\bar{N} > 0$ such that $\rho(\gamma(t_n), \bar{P}) < \bar{\delta}$ provided $n \geqslant \bar{N}$. Since the system (3.4) is autonomous, there is no loss of generality if we assume $\bar{P} = \bar{\gamma}(t_N)$ for any $N \geqslant \bar{N}$, fixed. Therefore, $\rho(\gamma(t_N), \bar{\gamma}(t_N)) < \bar{\delta}$ and so $\rho(\gamma(t), \bar{\gamma}(t)) < \sqrt{\varepsilon} M$ for all $t \in [t_N - T, t_N]$. Therefore, by the definition of ρ,

$$|S(t) - \bar{S}(t)| < \sqrt{\varepsilon} M \quad \text{for all } t \in [t_N - T, t_N]. \tag{8.8}$$

Define,

$$B = \{t \in [t_N - T, t_N]\colon S(t) \leqslant 1 - 2\sqrt{\varepsilon} M\},$$

$$G = \{t \in [t_N - T, t_N]\colon \bar{S}(t) \leqslant 1 - \sqrt{\varepsilon} M\},$$

$$\beta = \frac{1}{T} \mu(B) \quad \text{and} \quad \gamma = \frac{1}{T} \mu(G).$$

Then by Lemma 7.4, $\gamma \leqslant 6\sqrt{\varepsilon}$ provided $t_N > 2T$. Since $t_n \to \infty$ as $n \to \infty$ and the only restriction on N is that $N \geqslant \bar{N}$, there is no loss of generality if we assume $t_N > 2T$. By (8.8) $B \subset G$ and so

$$\beta \leqslant \gamma \leqslant 6\sqrt{\varepsilon}. \tag{8.9}$$

Also, if $\bar{t} \in [t_N - T, t_N] \backslash B$, defined to be B^c, then

$$\begin{aligned} S(\bar{t}) &> 1 - 2\sqrt{\varepsilon} M \\ &\geq 1 - 2\left(\frac{1-\lambda_2}{4M}\right) M \quad \text{by (8.5)} \\ &= \lambda_2 + (1-\lambda_2)/2. \end{aligned}$$

Therefore, by (8.4)

$$-1 + p_2(S(t)) \geq \bar{\varepsilon} \quad \text{for all } t \in B^c. \tag{8.10}$$

Integrating the x_2 equation from $t_N - T$ to t_N yields

$$x_2(t_N) = x_2(t_N - T) \exp\left(\int_{t_N - T}^{t_N} (-1 + p_2(S(v)))\, dv \right),$$

which implies that

$$\int_{t_N - T}^{t_N} (-1 + p_2(S(v)))\, dv < 0 \tag{8.11}$$

since by construction of the sequence $\{t_n\}$, $x_2(t_N - T) > x_2(t_N)$. However,

$$\begin{aligned} \int_{t_N - T}^{t_N} (-1 + p_2(S(v)))\, dv &= \int_B (-1 + p_2(S(v)))\, dv + \int_{B^c} (-1 + p_2(S(v)))\, dv \\ &\geq (-1)\mu(B) + \bar{\varepsilon}(T - \mu(B)) \quad \text{by (8.10)} \\ &= T(\bar{\varepsilon} - \beta(1 + \bar{\varepsilon})) \\ &\geq T(\bar{\varepsilon} - 6\sqrt{\varepsilon}(1 + \bar{\varepsilon})) \quad \text{by (8.6) and (8.9)} \\ &> T\left(\bar{\varepsilon} - 6\left(\frac{\bar{\varepsilon}}{6(1+\bar{\varepsilon})} \right)(1 + \bar{\varepsilon}) \right) \quad \text{by (8.5)} \\ &= 0 \end{aligned}$$

contradicting (8.11). Therefore, provided $\delta > 0$ is sufficiently close to zero so that (8.6) holds, $\underline{\lim}_{t \to \infty} x_2(t) > 0$.

That system (3.4) persists now follows immediately from Lemma 8.2. ☐

Remark 8.4. As with Theorem 7.1, we may make the stronger assertion that (3.4) is uniformly persistent.

One can actually show that $S(t) + x_2(t)$ is "*on the average*" as close to 1 as we like if q can be parametrized as in the hypothesis of the previous theorem and $\delta > 0$ is chosen sufficiently close to zero. The proof is similar to the proof of Lemma 7.3. From this we infer that as δ tends to zero the uniform lower bounds on both $\underline{\lim}_{t \to \infty} x_1(t)$ and $\underline{\lim}_{t \to \infty} y(t)$ tend to zero. We shall comment further on the ecological implications of this in the discussion in Sect. 10.

Theorem 8.5. *Assume* $1 - \lambda_2 - \delta p_1(\lambda_2) > 0$. *If* E_{S^*} *is globally asymptotically stable for* (3.4) *with respect to solutions for which* $x_{10} > 0$, $x_{20} = 0$ *and* $y_0 > 0$, *then system* (3.4) *is uniformly persistent.*

Proof. Let $\gamma(t)=(S(t), x_1(t), x_2(t), y(t))$ be a solution of (3.4) for which x_{i0}, $y>0$ $i=1,2$ and let Ω denote the associated omega-limit set. Since $1-\lambda_2-\delta p_1(\lambda_2)>0$ implies that $\lambda_1+\delta<1$, by Lemma 8.2 and Remark 8.4 it suffices to show that $\underline{\lim}_{t\to\infty} x_2(t)>0$.

Suppose $\underline{\lim}_{t\to\infty} x_2(t)=0$. Then there exists $\bar{P}=(\bar{S}, \bar{x}_1, 0, \bar{y})\in\Omega$, where $\bar{x}_1$, $\bar{y}>0$ by Lemma 8.2, and $\mathrm{cl}(\mathcal{O}(\bar{P}))\subset\Omega$. Note that $1-\lambda_2-\delta p_1(\lambda_2)>0$ implies that $S^*>\lambda_2$ and so (see Appendix A), E_{S^*} is unstable. Therefore $\{E_{S^*}\}\neq\Omega$ since $\gamma(0)\notin W^s(E_{S^*})=\{(S, x_1, x_2, y)\colon x_1>0,\ x_2=0,\ y>0,\ S\geqslant 0\}$ because $x_{20}>0$. Suppose $\bar{P}=E_{S^*}$. Since E_{S^*} is hyperbolic and $\{E_{S^*}\}\neq\Omega$, by Lemma 5.2 of [6] there exists $P^s\in(W^s(E_{S^*})\backslash\{E_{S^*}\})\cap\Omega$. Therefore, without loss of generality, assume $\bar{P}\neq E_{S^*}$. Since $\bar{P}\subset\mathscr{L}$ and $\bar{x}_1, \bar{y}>0$, the closure of the negative semi-orbit through $\bar{P}$ either contains E_1, E_{λ_1}, E_{λ_2} or it is not contained in $\mathbb{R}^4_+$. But $\underline{\lim}_{t\to\infty} y(t)>0$ and $\Omega\subset\mathbb{R}^4_+$ and so none of these alternatives is possible. This contradiction yields the result. □

One may obtain a number of technical conditions that guarantee the global stability of $E^3_{S^*}$ with respect to (7.1), by virtue of Theorem 8.5.

Corollary 8.6. *Assume* $1-\lambda_2-\delta p_1(\lambda_2)>0$. *Suppose that one of the following alternatives holds*:

(i) *H is differentiable and* $\lambda_1+\delta$ *is sufficiently close to* 1, *or*

(ii) *h is differentiable and* $h'(x)\geqslant 0$ *for all* $0<x<1-\lambda_1$, *or*

(iii) *q is twice differentiable and convex for* $0<x<1-\lambda_1$. *Then system* (3.4) *is uniformly persistent.*

By Theorem 5.2 it is possible to eliminate S from model (3.4) to obtain a three-dimensional Kolmogorov model that could be interpreted as two competitors and a predator with the predator predating on one of the competitors. In [15], Freedman and Waltman derive persistence criteria for general Kolmogorov models describing three interacting predator–prey populations as long as it can be shown that there are no nontrivial periodic orbits on the bounding coordinate planes. Our results contrast with theirs, since in our more restricted context, we are able to derive persistence criteria without having to exclude the possibility of periodic orbits. See in particular Theorem 8.3 and the example in the following section.

9. An example

That the orderly transfer of global stability from one critical point to another, as described in Sect. 6 (see Theorem 6.4 and 6.5), is not always the case for the food web (3.4) will be illustrated by means of an example. Recall that E_{S^*} is always locally asymptotically stable when it first enters the nonnegative cone (i.e. just as the sum $\lambda_1+\delta$ is decreased below 1). In the following example, as δ is decreased further, E_{S^*} loses its stability via a Hopf bifurcation before $\hat{E}_{\lambda_2}$ appears and $\hat{E}_{\lambda_2}$ is unstable as it enters $\mathbb{R}^4_+$. If δ is decreased sufficiently there is predator-mediated persistence and not only does the otherwise inferior competitor survive, but it survives at a higher concentration than that of its rival.

Example 9.1. In this example we assume that p_1 is Lotka-Volterra and q is Michaelis-Menten. More specifically, let

$$p_1(S) = 4S \quad (\text{i.e. } \lambda_1 = 1/4) \tag{9.1}$$

and

$$q(x_1) = x_1(\delta + 2\alpha)/(\delta(2\alpha + x_1)), \quad \text{where } \alpha = (\sqrt{13} - 2)/12 \approx 0.1338. \tag{9.2}$$

We also fix

$$\lambda_2 = 67/100. \tag{9.3}$$

Then, provided

$$\delta > 33/268 \approx 0.123 \quad (\text{i.e. } 1 - \lambda_2 - \delta p_1(\lambda_2) < 0) \tag{9.4}$$

$\hat{E}_{\lambda_2}$ does not lie in $\mathbb{R}^4_+$, but provided

$$\delta \leq 3/4 \quad (\text{i.e. } \lambda_1 + \delta \leq 1) \tag{9.5}$$

E_{S^*} does lie in $\mathbb{R}^4_+$. For this example

$$S^* = \lambda_1/(\lambda_1 + \delta) = 1/(1 + 4\delta) \tag{9.6}$$

and so if both (9.4) and (9.5) hold, $S^* < \lambda_2$. Therefore, by (A2) the local stability of E_{S^*} depends on the sign of

$$y^*(\delta q'(\delta) - 1)/\delta + \delta p_1'(S^*). \tag{9.7}$$

If (9.7) is positive, E_{S^*} is locally asymptotically stable and if (9.7) is negative, then E_{S^*} is unstable. With p_1 and q satisfying (9.1) and (9.2), (9.7) equals $(\delta(16\delta^2 + 32\alpha\delta + 8\alpha - 3))/((1 + 4\delta)(2\alpha + \delta))$. Thus the sign of (9.7) depends on the sign of $g(\delta) = 16\delta^2 + 32\alpha\delta + 8\alpha - 3$. Since $\alpha > 0$, $g(\delta)$ is a strictly increasing function of δ. Noting that $g(\alpha) = 0$, it follows that E_{S^*} is locally asymptotically stable for $\delta > \alpha$ and is unstable for $\delta < \alpha$. For $\delta = \alpha$ both (9.4) and (9.5) are satisfied and so E_{S^*} loses its stability before $\hat{E}_{\lambda_2}$ appears in the nonnegative cone. At $\alpha = \delta$, the characteristic equation can be shown to have two real, negative roots and two pure imaginary roots and the real part of the complex conjugate pair of roots crosses zero transversely at $\delta = \alpha$. Thus the change in stability at $\delta = \alpha$ is via a Hopf bifurcation. Numerical results seem to indicate that the bifurcating periodic orbits exist for $\delta < \alpha$ and are stable.

Figures 1 and 2 illustrate this Hopf bifurcation in the case that

$$p_2(S) = 150S/(67 + 50S). \tag{9.8}$$

In both figures we take

$$S_0 = 0.4, \qquad x_{10} = 0.3, \qquad x_{20} = 0.2 \quad \text{and} \quad y_0 = 0.1. \tag{9.9}$$

In Fig. 1, $\delta = 0.3 > \alpha$. The solution converges to E_{S^*}. In Fig. 2, $\delta = 0.13 < \alpha$ and

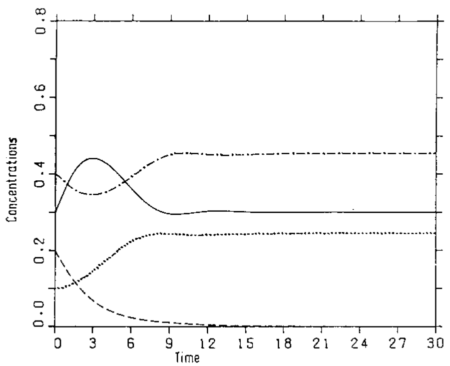

Fig. 1. E_{S^*} is asymptotically stable ($\delta = 0.3 > \alpha$). —— x_1; - - - x_2; - · - S; · · · · y

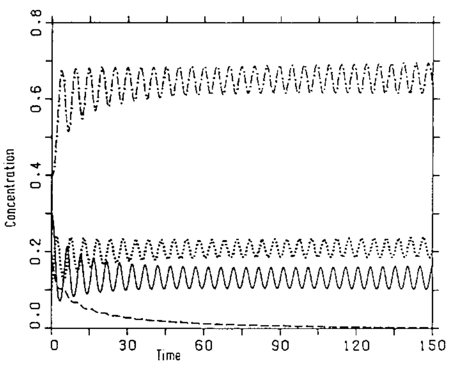

Fig. 2. E_{S^*} is unstable and $\hat{E}_{\lambda_2} \notin \mathcal{R}^4_+$ ($\delta = 0.13 < \alpha$). —— x_1; - - - x_2; - · - S; · · · · y

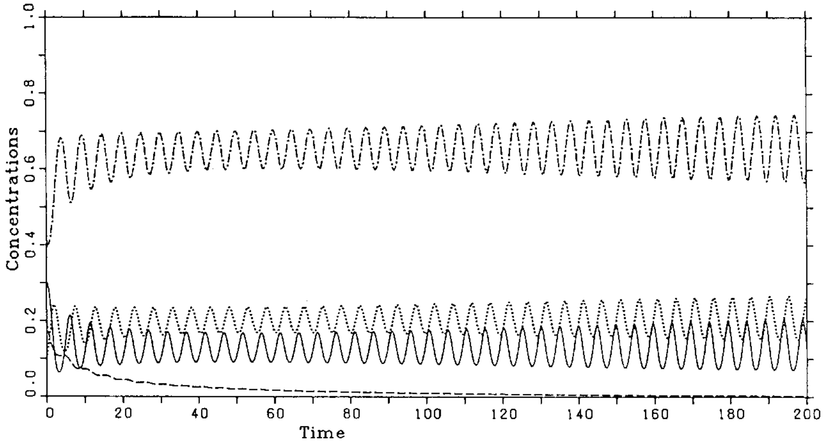

Fig. 3. $\hat{E}_{\lambda_2} \in \mathbb{R}^4_+$ but is unstable ($\delta = 0.12$). —— x_1; - - - x_2; - · - S; · · · · y

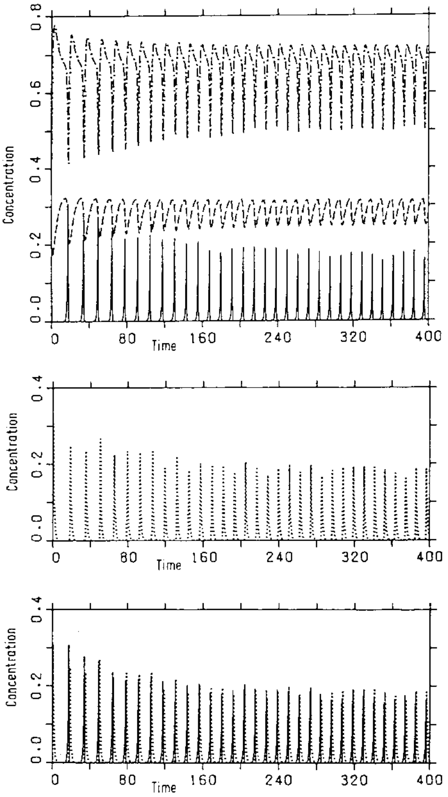

Fig. 4. Predator-mediated persistence ($\delta = 0.014$). —— x_1; - - - x_2; - · - S; · · · · y

so δ satisfies (9.4) and (9.5). Therefore $\hat{E}_{\lambda_2} \notin \mathbb{R}^4_+$ and E_{S^*} is unstable. This figure seems to depict a stable periodic solution.

Figures 3 and 4 also depict solutions with $p_2(S)$ defined by (9.8) and initial conditions (9.9). In Fig. 3, $\delta = 0.12$ and so $\hat{E}_{\lambda_2} \in \mathbb{R}^4_+$, but δ is close to the value at which $\hat{E}_{\lambda_2}$ and E_{S^*} coalesce. Clearly $\hat{E}_{\lambda_2}$ is unstable.

In the final graph, Fig. 4, we reduce δ even further, to $\delta = 0.014$. For this value of δ we obtain persistence. Note that not only does x_2 survive, but it survives at higher concentrations than its rival, x_1. Also, a good deal of the time the concentrations of x_1 and y are very close to zero. Thus each of these populations is in danger of a small stochastic event causing extinction in finite time.

10. Discussion

We have been concerned with the qualitative behaviour that can result when a predator invades a chemostat in which two populations of microorganisms are competing for a single, essential, growth-limiting nutrient. We are also interested in the 3-dimensional food chain that results when the competitor that is inferior in the absence of predation is eliminated. For the most part we consider general monotone dynamics for microbial-nutrient dynamics. We are however, motivated by results obtained by considering three common prototypes for monotone functional responses: Lotka-Volterra, Michaelis-Menten, and multiple saturation.

In general we can summarize the results of this paper as follows. As various parameters are decreased, the model exhibits a sequence of different stages of global behaviour. At each stage, conditions have become sufficiently favourable for a new population to survive. Eventually the model predicts persistence of the entire food web.

We obtain our most complete results in the case that a Lotka-Volterra response function is used to describe prey utilization by the predator and each response function describing competitor-substrate interaction is of either Lotka-Volterra or Michaelis-Menten form. In this case there is an unbroken chain of transference of global stability from one critical point to another as certain parameters decrease.

If we relax the assumptions on the functional responses further to allow quite general monotone kinetics, there is still a transference of global stability from E_1 to E_{λ_1} to E_{S^*} as described above. However, the chain can be broken at this point. What one can however show is that if predation is voracious enough the entire food web persists.

If we interpret the thresholds λ_1, $\lambda_1+\delta$, and $1-\lambda_1-\delta p_1(\lambda_2)$ in terms of their counterparts for the unscaled model, we gain insight into the biology of the situation. Decreasing a λ_i can be achieved either by increasing S^0, the concentration of nutrient in the feed bottle, by decreasing D, the dilution rate or by selecting a competitor that is more efficient at low concentrations of substrate. Decreasing δ can be achieved by increasing S^0, by decreasing D or by selecting a predator that is more efficient at low concentrations of the prey. However, δ can also be decreased by selecting a prey with larger growth yield constant y_1. Thus, according to the predictions of this model, there are a number of ways that an experimenter can make adjustments in order to influence the outcome of the microbial interactions in a chemostat. Also, he should be able to predict the outcome in advance, based on the measurement of certain parameters and the measurement of these parameters can be achieved by studying the interactions between pairs (i.e. competitor-substrate pairs or the predator-prey pair). Therefore, the predictions of this model can be tested in the laboratory in a way analogous to that used by Hansen and Hubbell [20] to verify the predictions of the model analyzed by Hsu, Hubbell and Waltman [21].

In [5] we showed that in the absence of a predator, one competitor always outcompetes his rival (i.e. there is at most one survivor). This model evidently confirms current ecological thinking that predation can be responsible for diversity in ecosystems. Levin [26] explains: "*Two species can coexist at a stable equilibrium if each is limited by an independent combination of predation and resource limitation, since then two independent factors are serving to limit two species.*" Paine [32] gives experimental results that actually show that the removal of one predator, Pisaster, resulted in a collapse from a 15 species to an 8 species food web. For other examples of competitive coexistence resulting from predation see [10, 11, 30, 33, 34, 48].

What can be said about the possibility of invasion by a predator actually causing reversal in the outcome of competition between two rivals? In the strictly deterministic sense, invasion by a predator does not reverse the outcome of the competition. However, at a sufficiently high level of predation, the loser in pure competition survives at a more abundant concentration on the average than his rival, who periodically plunges to dangerously low levels (see Fig. 4). So from a stochastic point of view it is conceivable that there would be a reversal of competitive outcome.

With respect to Rosensweig's paradox of enrichment [35], it is also noteworthy that this model predicts that the more the environment is enriched by increasing the concentration of substrate in the feed bottle, the more diverse the ecosystem that persists, even though, as Saunders and Bazin [36] point out, enrichment can cause all the equilibria to destabilize.

Appendix: Linear analysis of the food web and food chain models

A. Linear analysis —food web model

We summarize the local stability of each of the critical points E_1, E_{λ_1}, E_{λ_2}, E_{S^*}, $\hat{E}_{\lambda_2}$.

a. E_1 is asymptotically stable if $\lambda_1, \lambda_2 > 1$ and is unstable if either $\lambda_1 < 1$ or $\lambda_2 < 1$.
b. E_{λ_2} is always unstable.
c. E_{λ_1} is asymptotically stable provided $1 - \delta < \lambda_1 < 1$ and is unstable if $\lambda_1 + \delta < 1$.
d. E_{S^*} is asymptotically stable provided that

$$\text{(i)} \quad S^* < \lambda_2,$$

and

$$\text{(ii)} \quad y^*(\delta q'(\delta) - 1)/\delta + \delta p_1'(S^*) > 0. \tag{A2}$$

If the inequality in (i) or (ii) is reversed then E_{S^*} is unstable. Note that,

$$\delta q'(\delta) - 1 = \delta^2 h'(\delta),$$

so that (ii) is equivalent to

$$\text{(ii)}' \quad y^* h'(\delta) + p_1'(S^*) > 0. \tag{A3}$$

e. $\hat{E}_{\lambda_2}$ is locally asymptotically stable provided

$$\text{(i)} \quad C_0 > 0, \qquad C_1 > 0 \quad \text{and} \quad C_2 > 0, \tag{A4}$$

and

$$\text{(ii)} \quad \Delta_2 = C_2 C_1 - C_0 > 0, \tag{A5}$$

where c_0, c_1, c_2 are the coefficients of the associated characteristic equation, and is unstable if any inequality in (i) or (ii) is reversed. One can show that provided $\hat{E}_{\lambda_2}$ lies in the positive (S, x_1, x_2, y) cone and $\delta q'(\delta) \geqslant 1$ then $\hat{E}_{\lambda_2}$ is locally asymptotically stable. In particular this applies if $q(x_1)$ is Lotka-Volterra, i.e. $q(x_1) = x_1/\delta$ since then $\delta q'(\delta) = 1$. However, if $q(x_1)$ satisfies Michaelis-Menten kinetics, i.e. $q(x_1) = \mu x_1/\delta(\mu - 1) + x_1$ where $\mu > 1$, then $\delta q'(\delta) = (\mu - 1)/\mu < 1$.

B. Linear analysis —food chain model

We summarize the local stability of each of the critical points E_1^3, $E_{\lambda_1}^3$, $E_{S^*}^3$.

a. E_1^3 is asymptotically stable if $\lambda_1 > 1$ and is unstable if $\lambda_1 < 1$.
b. $E_{\lambda_1}^3$ is asymptotically stable provided $1 - \delta < \lambda_1 < 1$ and is unstable if $\lambda_1 + \delta < 1$.

c. $E^3_{S^*}$ is asymptotically stable provided

$$y^*(\delta q'(\delta)-1)/\delta+\delta p_1'(S^*)>0 \tag{B1}$$

and is unstable if the inequality is reversed.

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