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Persistence Criteria for a Chemostat with Variable Nutrient Input

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The standard single-species chemostat model is modified to include a variable nutrient input which is assumed only to be nonnegative, bounded, and continuous. We obtain necessary and sufficient conditions for persistence and show that all solutions of any given chemostat system have the same long-time behavior independent of the initial conditions. Counterexamples shed light on the results obtained. © 2001 Academic Press

The equations considered here are

$$s' = aq(t) - as - p(s)x, \tag{1a}$$

$$x' = -bx + p(s)x, \tag{1b}$$

where a and b are positive constants and q is a continuous bounded function from $[0, \infty)$ to $[0, \infty)$. It is assumed that $p'(s)$ is positive and continuous for $s \geqslant 0$ and that

$$p(0) = 0, \qquad s(0) = s_0 > 0, \qquad x(0) = x_0 > 0.$$

The physical and biological background of the chemostat is discussed at length in the accompanying references. Suffice it to say here that $s(t)$, $x(t)$ denote respectively the concentrations of nutrient and microorganisms in

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the growth vessel while $q(t)$ is the concentration of the nutrient in the input, all at time t. The function $p(s)$ is the per capita nutrient uptake rate of the microorganism when the concentration is s. The constants a, b are respectively the dilution rate (flow divided by volume) and the removal rate of the microorganism.

Definitions of persistence, often characterized by the words *weak*, *strong*, and *average*, are given in one or another of [3–5, 10, 13, 14, 22, 23]. These definitions are repeated as needed below. Chemostats with periodic inputs are studied in [7, 11, 19, 21], those with periodic removal rates in [2], and persistence is investigated in [4, 6, 16]. If q is constant or periodic our results agree with [12, 24] and [7] respectively. However, our assumptions are much weaker than those in [7, 12, 24], and neither the results nor the counterexamples are in any prior work known to us.

PRELIMINARIES

The expressions lim, lim inf, lim sup pertain to behavior as $t \to \infty$. A condition holds for large t, or for $t \gg 1$, if there exists T such that it holds for $t > T$. We use the Hardy–Littlewood notation $o(1)$ to denote a function of t with limit 0. It is assumed throughout that x, s satisfy (1).

THEOREM 1. *The solution x, s exists on $[0, \infty)$. It satisfies $x > 0$, $s > 0$, and s, x, s', x', x'' are all bounded.*

Proof. Local existence and uniqueness are assured because $p(s)$ is locally Lipschitzian. Let the interval of existence be $I = [0, d)$ with $d \leqslant \infty$ and let $J = [0, c)$ where $0 < c < d$. On J the functions $s, x, p(s), p'(s)$ are all bounded, so $s' \geqslant -Ks$, $x' \geqslant -Kx$, where $K = K(J)$ is constant. Hence $s, x > 0$ on J, and letting $c \to d$ gives the same on I. By the addition of (1a) (1b),

$$(s+x)' = aq - as - bx \leqslant aM - m(s+x),$$

where $M = \sup q$ and $m = \min(a, b)$. Thus

$$m(x+s) > aM \Rightarrow (s+x)' < 0,$$

so $s + x \leqslant \max(s_0 + x_0, aM/m)$. This uniform bound for $x + s$ gives the same bound for x, s and shows that the solution can be extended to $[0, \infty)$. Boundedness of s' and x' follows from the differential equations and boundedness of x'' then follows when (1b) is differentiated. This completes the proof and yields the explicit inequality

$$\limsup\,(s+x) \leqslant \frac{a}{\min(a, b)} \limsup q(t).$$

The following lemma will be used with $k=a$ or $k=b$ and with $v=xp(s)$. Note that v' is bounded by Theorem 1.

Lemma 1. *For $t>0$ let $u'+ku=v$ where $k>0$ is constant, $v \in C^1$, and both v and v' are bounded. Then u, u', u'' are bounded and*

$$\lim u(t)=0 \Leftrightarrow \lim v(t)=0. \tag{2}$$

Proof. The formula for u in terms of v gives the well-known inequalities

$$\liminf v(t) \leqslant k \liminf u(t) \leqslant k \limsup u(t) \leqslant \limsup v(t).$$

Namely, for $0<T<t$, we have

$$u(t)=e^{-kt} \int_T^t e^{ks} v(s)\, ds+o(1).$$

If $\varepsilon>0$ and T is sufficiently large, $v(s)$ in the integrand is between

$$\liminf v(t)-\varepsilon \qquad \text{and} \qquad \limsup v(t)+\varepsilon,$$

and the result follows from this. The inequalities lead to all but the implication $\Rightarrow$ in (2). The latter follows from a theorem of Littlewood (originally due to Hadamard) to the effect that as $t \to \infty$

$$u(t)=o(1), \qquad u''(t)=O(1) \Rightarrow u'(t)=o(1).$$

A short proof of the Hadamard–Littlewood theorem is outlined in [15]. An extension to derivatives of arbitrary order and vector-valued functions is given in [17], where the connection of these results with differential equations is also mentioned.

Lemma 2. *Let z be defined by $z'+az=aq$, $z(0)=0$. Then either $s(t)<z(t)$ for all large t or $s(t)>z(t)$ for all $t>0$. In the second case $\lim x(t)=0$.*

Proof. Suppose $s(t_0)<z(t_0)$ at some value $t_0>0$. We claim that $s(t)<z(t)$ for all $t>t_0$. If not, let t_1 be the smallest value $t>t_0$ at which

$s(t)=z(t)$. Then $s(t_1)=z(t_1)$, $s'(t_1)\geqslant z'(t_1)$, and the differential equations at t_1 lead to a contradiction,

$$s' = a(q-s) - p(s)\, x = a(q-z) - p(z)\, x = z' - p(z)\, x < z'.$$

If $s(t_0)=z(t_0)$ at some value $t_0>0$ then $s'(t_0)<z'(t_0)$ by the differential equations. So $s(t)<z(t)$ at nearby points with $t>t_0$, and the conclusion follows again. The only alternative is to have $s(t)>z(t)$ for all $t>0$, in which case we use the fact that the equation

$$(s-z)' = -a(s-z) - p(s)\; x \tag{3}$$

implies $(s-z)'\leqslant -a(s-z)$. Hence (being positive) $s-z$ approaches 0 as $t\to\infty$. Lemma 1 gives $p(s)\, x\to 0$ and, applying the lemma again to $x' = -bx + p(s)\, x$, we get $x\to 0$. This completes the proof.

For any continuous function f we define the average $\bar{f}$ by

$$\bar{f}(t) = \frac{1}{t}\int_0^t f(s)\, ds.$$

Lemma 3. *There exist positive constants A and B such that, within terms of order* $1/t$,

$$A\bar{x}(t) + \frac{\ln x(t)}{t} \leqslant \overline{p(z)}\,(t) - b \leqslant B\bar{x}(t).$$

Proof. Referring to Lemma 2, suppose $s(t)<z(t)$ for all large t. By the mean-value theorem

$$p(z) - p(s) = p'(\xi)(z-s)$$

where ξ is between z and s. Since z and s are bounded there are positive constants K, L, independent of ξ, such that $K\leqslant p'(\xi)\leqslant L$. Hence

$$K(z-s)\leqslant p(z)-p(s)\leqslant L(z-s), \qquad t\gg 1.$$

If $s(t)>z(t)$ for all t we change L, K so that $L\leqslant p'(\xi)\leqslant K$ and get the same inequality again. Hence in both cases

$$K(\bar{z}-\bar{s})\leqslant \overline{p(z)} - \overline{p(s)} \leqslant L(\bar{z}-\bar{s}), \tag{4}$$

within terms of order $1/t$; this error term is needed because the inequalities are guaranteed only for large t. Within terms of the same order we have also

$$\overline{p(s)}\,(t) = b + \frac{\log x(t)}{t}, \qquad a(\bar{z} - \bar{s}) = b\bar{x}.$$

The first of these is found when $x' = -bx + p(s)\,x$ is divided by x and integrated; the second by integrating $x' + s' - z' = -as - bx + az$, using the fact that z is bounded by Lemma 1 and x, s by Theorem 1. Lemma 3 now follows with $A = Kb/a$ and $B = Lb/a$. The term involving $\log x(t)$ on the right can be dropped because this term is $\leqslant c/t$, where c is some constant. On the left it can be dropped only if $\liminf x(t)\, e^{\delta t} > 0$ for all $\delta > 0$.

Concluding this introductory discussion, we mention that the equations

$$s' + as = aq - x' - bx, \qquad x' + bx = aq - s' - as$$

give either unknown s, x in terms of the other by quadrature. In particular, if $a = b$ the functions $s + x$ and z satisfy the same linear differential equation, so

$$x(t) + s(t) = z(t) + (x_0 + s_0)\, e^{-at}, \qquad a = b.$$

If $y' + ay = (b - a)\, x$ and $y(0) = -s_0 - x_0$, then $u = s + x + y - z$ satisfies $u' + au = 0$ and $u(0) = 0$. Hence $u = 0$, so $x + y + s = z$. These remarks shed light on (1) but are not used in the following.

PERSISTENCE

Clearly $\liminf x(t) \leqslant \liminf \bar{x}(t) \leqslant \limsup \bar{x}(t) \leqslant \limsup x(t)$; the trivial proof is left to the reader. If any one of these four expressions is positive for all solutions x, this situation is characterized by the term *persistence*. Positivity of the first, second, third, and fourth expressions is commonly referred to as *strong persistence*, *strong average persistence*, *weak average persistence*, and *weak persistence*, respectively. In an obvious notation

$$\text{SP} \Rightarrow \text{SAP} \Rightarrow \text{WAP} \Rightarrow \text{WP} \Rightarrow \text{not NP},$$

where NP means *no persistence* in the sense that $\lim x(t) = 0$. We define

$$w(t) = p(z(t))$$

where

$$z(t) = ae^{-at} \int_0^t e^{ar} q(r)\, dr$$

and establish

THEOREM 2. *The following five implications hold for all solutions x:*

(a) $\limsup \bar{x}(t) > 0 \Leftrightarrow \limsup \bar{w}(t) > b$,

(b) $\limsup \bar{w}(t) < b \Rightarrow \lim x(t) = 0$,

(c) $\liminf \bar{w}(t) > b \Rightarrow \liminf \bar{x}(t) > 0$,

(d) $\liminf x(t) > 0 \Rightarrow \liminf \bar{w}(t) > b$.

Conditions (abcd) pertain to WAP, NP, SAP, and SP, respectively.

Proof. The conclusion of Lemma 3 gives

$$A\bar{x}(t) + \frac{\ln x(t)}{t} \leqslant \bar{w}(t) - b \leqslant B\bar{x}(t), \tag{5}$$

only within terms of order $1/t$, but these terms can be ignored in the following analysis. The implications ($a \Leftarrow$) and (c) follow from the right-hand inequality in (5) while (b) and (d) follow from the left-hand inequality in (5). (For (b), note that $\bar{x} \geqslant 0$.) Using the sequence $\{r_n\}$ provided by Lemma 4 below, we see that ($a \Rightarrow$) also follows from the left-hand inequality (5).

LEMMA 4. *If* $\limsup \bar{x}(t) > \delta > 0$, *then there exists a sequence $r_n \to \infty$ on which $x(r_n) \geqslant \delta$ and $\bar{x}(r_n) \geqslant \delta$.*

Proof. The following proof uses only the fact that x is continuous; actually, local integrability suffices. The hypothesis implies $\limsup x(t) > \delta$. Find a point t_1 at which $x(t_1) \geqslant \delta$, then a point $s_1 > t_1 + 1$ at which $\bar{x}(s_1) \geqslant \delta$, then $t_2 > s_1 + 1$ at which $x(t_2) \geqslant \delta$, then $s_2 > t_2 + 1$ at which $\bar{x}(s_2) \geqslant \delta$, and so on. If $x(s_n) \geqslant \delta$ take $r_n = s_n$. Otherwise, go back towards $t = 0$ from s_n until you first reach a point r_n at which $x(r_n) = \delta$. Then $t_n \leqslant r_n \leqslant s_n$ and $x(t) < \delta$ on the interval (r_n, s_n). We have

$$\delta s_n \leqslant \int_0^{s_n} x(t)\, dt \leqslant \int_0^{r_n} x(t)\, dt + \int_{r_n}^{s_n} \delta\, dt = \int_0^{r_n} x(t)\, dt + \delta(s_n - r_n),$$

and hence

$$\bar{x}(r_n) = \frac{1}{r_n} \int_0^{r_n} x(t)\, dt \geqslant \delta.$$

This completes the proof.

Theorem 2 implies further results that seem at first glance to be different from (abcd). For example, (a $\Leftarrow$) yields the second implication in

$$\lim x(t) = 0 \Rightarrow \limsup \bar{x}(t) = 0 \Rightarrow \limsup \bar{w}(t) \leqslant b$$

and (b) gives $\limsup x(t) > 0 \Rightarrow \limsup \bar{w} \geqslant b$.

By (d) the condition $\liminf \bar{w}(t) > b$ is necessary for strong persistence, but an example given later shows that it is not sufficient. We now give a uniform version of the inequality $\liminf \bar{w}(t) > b$ that is both necessary and sufficient. To this end we set

$$\bar{f}(t_1, t_2) = \frac{1}{t_2 - t_1} \int_{t_1}^{t_2} f(s)\, ds, \qquad 0 \leqslant t_1 < t_2,$$

where f is continuous, and introduce the following definition:

DEFINITION. The condition $\bar{f}(t_1, t_2) > b$ holds uniformly for large values of the arguments if there exist positive constants η, T such that

$$t_1 > T, \qquad t_2 - t_1 > T \Rightarrow \bar{f}(t_1, t_2) > b + \eta.$$

Persistence theorems involving the asymptotic behavior of averages are given in [1, 18] and some of them depend on a uniformity similar to that in the above definition. However, the equations considered in these references are different from (1) and there is no overlap of those results with ours.

THEOREM 3. *We have* $\liminf x(t) > 0$ *if and only if* $\bar{w}(t_1, t_2) > b$ *holds uniformly for large values of the arguments.*

Proof. Throughout the following discussion,

$$T < t_1 < t_1 + T < t_2, \qquad L(t_1, t_2) = \frac{\log x(t_2) - \log x(t_1)}{t_2 - t_1}. \tag{6}$$

Here $T > 1$ is at least as large as required in the definition and will be further increased as needed.

We note first that there are positive constants A, B such that, within terms of order $1/(t_2 - t_1)$,

$$A\bar{x}(t_1, t_2) + L(t_1, t_2) \leqslant \bar{w}(t_1, t_2) - b \leqslant B\bar{x}(t_1, t_2) + L(t_1, t_2). \tag{7}$$

The proof is virtually identical to the proof of Lemma 3, the role of $(0, t)$ being taken by (t_1, t_2). In fact, if T is sufficiently large, (7) holds without any error term, giving a slight simplification. Unlike $x(0)$, however, $x(t_1)$ may be arbitrarily close to 0. That is why $L(t_1, t_2)$ is needed on the right of the inequalities as well as on the left.

Suppose now that $\liminf x(t) > \delta > 0$. Then $L(t_1, t_2)$ is bounded and, if T is sufficiently large, $\bar{x}(t_1, t_2) \geqslant \delta$. Thus the left-hand inequality (7) with its error term gives

$$\bar{w}(t_1, t_2) - b \geqslant A\delta - \frac{C}{t_2 - t_1},$$

where C is a positive constant. The right side is positive if T is sufficiently large and this proves half of Theorem 3.

Suppose next that $\bar{w}(t_1, t_2) > b$ holds uniformly for large values of the arguments. If $\lim x(t) = 0$ (a possibility we want to exclude) then we fix t_1 and let $t_2 \to \infty$. Since $x(t_2) < x(t_1)$ for large t_2, the right-hand inequality (7) with its error term yields

$$\bar{w}(t_1, t_2) - b \leqslant B\bar{x}(t_1, t_2) + \frac{C}{t_2 - t_1}, \tag{8}$$

where C is constant. As $T \to \infty$ in (6) the right-hand side of (8) tends to 0 and this contradicts the hypothesis. The upshot is that $\limsup x(t) > 0$. If the conclusion fails we also have $\liminf x(t) = 0$, and both of these conditions are assumed from now on.

Let ε and δ be constants satisfying $0 < \varepsilon < \delta < \limsup x(t)$. We can find t_0, t, t_3 with $T < t_0 < t < t_3$ such that

$$x(t_0) > \delta, \qquad x(t) < \varepsilon, \qquad x(t_3) > \delta.$$

This follows from $\limsup x(t) > \delta$, $\liminf x(t) = 0$. Starting at t, go back toward t_0 until you first reach a point t_1 at which $x(t_1) = \delta$. Then go forward from t toward t_3 until you first reach a point t_2 at which $x(t_2) = \delta$. Thus

$$T < t_1 < t < t_2, \qquad x(t_1) = x(t_2) = \delta, \qquad x(t) < \varepsilon.$$

Since $x(t_1)=x(t_2)$ we have $L(t_1, t_2)=0$, so (8) holds. Since $x(t)\leqslant\delta$ on (t_1, t_2) we have also $\bar{x}(t_1, t_2)\leqslant\delta$. The inequality $x'\geqslant -bx$ gives

$$x(t)\geqslant x(t_1)\, e^{-b(t-t_1)},$$

hence

$$b(t-t_1)\geqslant\log\delta-\log\varepsilon.$$

Using $t_2-t_1>t-t_1$ and the right-hand inequality (8), we get

$$\bar{w}(t_1, t_2)-b\leqslant B\delta+\frac{bC}{\log\delta-\log\varepsilon}.$$

By picking first δ and then ε the right-hand side can be made arbitrarily small, contradicting the hypothesis.

COUNTEREXAMPLES

Taking $p(s)=s$, we will construct counterexamples to show that the foregoing results are in various respects sharp. The equations are now

$$s'=aq(t)-(a+x)\,s, \qquad x'=-bx+sx$$

and the technique is to prescribe x in such a way that q satisfies our original hypotheses. Substituting $s=(x'/x)+b$ into the first equation yields

$$aq=\left(\frac{x'}{x}\right)'+(a+x)\left(\frac{x'}{x}+b\right). \tag{9}$$

If q as given by this equation is continuous, bounded, and positive on $(0, \infty)$, the solution x provides an example with that q and is termed *admissible*. Actually, we will choose x so that $\inf q>0$, although the original hypothesis requires only $q\geqslant 0$.

For $|t|<\infty$ let $f(t)$ be a C^2 function with support on the interval $(-1, 1)$ and satisfying $f(t)>0$ on this interval. We also assume

$$|f'(t)|<1, \qquad |f''(t)|<1.$$

Our examples have the form

$$x(t)=g(t)+h(t)$$

where

$$g(t)=\sum_{n=1}^{\infty} f\left(\frac{t-a_n}{n}\right)$$

and h is a positive decreasing C^2 function that tends to 0. It is required further that

$$a_1 \geqslant 1, \qquad a_{n+1}-a_n \geqslant 2n+1, \qquad n=1, 2, 3, ...$$

The graph of g is a series of arches and the above condition keeps them off one another's feet, so

$$g(t)=f\left(\frac{t-a_n}{n}\right), \qquad |t-a_n| \leqslant n. \tag{10}$$

This shows that $x \in C^2$ and that x is bounded. Also, when (10) holds,

$$\left|\frac{x'(t)}{x(t)}\right| \leqslant \frac{1}{nh(t)}+\left|\frac{h'(t)}{h(t)}\right|, \qquad \left|\frac{x''(t)}{x(t)}\right| \leqslant \frac{1}{n^2 h(t)}+\left|\frac{h''(t)}{h(t)}\right|.$$

Noting that $h(t) \geqslant h(a_n+n)$ for $|t-a_n|<n$, we want to construct $h(t)$ such that

$$\lim \left(\frac{h'(t)}{h(t)}\right)=0, \qquad \lim \left(\frac{h''(t)}{h(t)}\right)=0, \quad \sqrt{n}\, h(a_n+n) \geqslant 1.$$

The last condition is needed for all $n \geqslant 1$. Once this is done Eq. (9) together with

$$\left(\frac{x'}{x}\right)'=\frac{x''}{x}-\left(\frac{x'}{x}\right)^2$$

gives $\liminf q(t) \geqslant b$. Hence for T sufficiently large $x(t+T)$ is admissible. Alternatively, we can consider $x(t)$ only for $t \geqslant T$, letting T rather than 0 take the role of the initial-value point. In either case the introduction of T has no effect on our conclusions, so we carry out calculations on $[0, \infty)$ as before.

To construct $h(t)$, let $j(t)$ be the obvious piecewise linear function whose graph contains the points $(a_n+n, 1/\sqrt{n})$ and let $j(t)=1$ on $(0, a_1)$. The following lemma gives what is required:

Lemma 5. *Let $j(t)$ be any positive function with* $\lim j(t)=0$. *Then there exists a decreasing C^2 majorant $h \geqslant j$ such that $h(t)$, $h'(t)/h(t)$, and $h''(t)/h(t)$ all tend to* 0.

Proof. Set $i(t) = \sup_{s \geqslant t} j(s)$, $m(t) = \bar{i}(t)$, $k(t) = \bar{m}(t)$, and $h(t) = \bar{k}(t)$. Then $i(t)$ and $m(t)$ are decreasing, $m(t) \geqslant i(t) \geqslant j(t)$, $\lim m(t) = 0$, and

$$0 < k \leqslant h, \qquad 0 < m \leqslant k, \quad tk' = m - k, \quad th' = k - h, \quad th'' = k' - 2h'.$$

Hence $t\,|h'/h| < 1$ and $t^2\,|h''/h| < 2$. The equation $th' = k - h$ yields $h' \leqslant 0$, and $\lim m(t) = 0 \Rightarrow \lim k(t) = 0 \Rightarrow \lim h(t) = 0$. This completes the proof.

We now turn to the construction of examples. Setting $u = (t - a_n)/n$ gives

$$\int_{a_n - n}^{a_n + n} f\left(\frac{t - a_n}{n}\right) dt = nA,$$

where

$$A = \int_{-1}^{1} f(t)\, dt.$$

Hence for $|t - a_n| \leqslant n$

$$\int_0^t g(t)\, dt = \frac{n^2}{2} A + E,$$

where

$$|E| \leqslant nA/2.$$

The same holds for $a_n + n \leqslant t \leqslant a_{n+1} - (n+1)$. Since $a_n \geqslant n^2$ the term E does not affect the limiting behavior of $\bar{g}(t)$ and is ignored here.

Part of the content of Lemma 5 is that $h(t)$ can approach 0 as slowly as desired. For example, we can assume $h(t) > 1/t$. When this holds Lemma 3 gives

$$A\bar{x}(t) \leqslant \bar{w}(t) - b \leqslant B\bar{x}(t) \tag{11}$$

within terms of order $(\log t)/t$.

Example 1. We have a solution that exhibits strong average persistence but not strong persistence; in other words, $\liminf \bar{x}(t) > 0$ but $\liminf x(t) = 0$. Here we take $a_n = n^2$, so the successive arches in the graph of $g(t)$ are adjacent. Then $\lim \bar{x}(t) = A/2$ and $x(t) = h(t)$ at the values t where two arches meet. Together with (11), this example shows that the condition $\liminf \bar{w}(t) > b$ is not sufficient to ensure $\liminf x(t) > 0$.

EXAMPLE 2. We have a solution that exhibits weak persistence but not weak average persistence; in other words, $\limsup x(t) > 0$ but $\lim \bar{x}(t) = 0$. It is easily checked that the choice $a_n = n^3$ yields both conditions.

EXAMPLE 3. We have a solution that exhibits weak but not strong average persistence; in other words, $\limsup \bar{x}(t) > 0$ but $\liminf \bar{x}(t) = 0$. Here we take $a_n = n^2$ up to n_1, then n^3 up to n_2, then n^2 up to n_3, and so on. Since the behavior of $x(t)$ on a finite interval $(0, n_k)$ does not affect $\liminf \bar{x}(t)$ or $\limsup \bar{x}(t)$, we can pick n_1 so large that $\bar{x}(n_1)$ is close to $A/2$. Then we can pick n_2 so large that $\bar{x}(n_2)$ is close to 0, then n_3 so large that $\bar{x}(n_3)$ is close to $A/2$, and so on.

Each of these examples is based on a single function $x(t)$, although the example allows all positive values of a and b. Namely, we just start at some value $t = T$ which may depend on a and b but otherwise does not affect $x(t)$. In the next section we show that the ratio x_1/x_2 of two solutions is bounded away from 0 and ∞. Hence every solution has essentially the same behavior as the particular solution given in the example.

If $b = a \gg 1$ one can construct explicit counterexamples as elementary functions. For $t \geqslant 1$, as can be assumed without loss of generality, the first of the following solutions exhibits strong average persistence but not strong persistence, while the second exhibits weak persistence but not weak average persistence:

$$x(t) = 1 + \sin(\log t) + \frac{1}{t}, \qquad x(t) = e^{-t - t\sin(\log t)}.$$

However, the verification of admissibility and of the stated behavior is rather long (especially in the second case) and the condition $a = b \gg 1$ is extremely restrictive. By contrast, the examples given above require little calculation and apply for all positive a, b.

COMPARISON

Let s_1, x_1 and s_2, x_2 be two solutions of (1) and set

$$S = s_1 - s_2, \qquad X = x_1 - x_2, \quad R = \frac{x_1}{x_2}, \quad P = p(s_1)\,x_1 - p(s_2)\,x_2.$$

The first two of the following equations are obtained from (1) by subtraction and the third by differentiating $\log R = \log x_1 - \log x_2$:

$$S' + aS = -P, \tag{12a}$$

$$X' + bX = P, \tag{12b}$$

$$\frac{d}{dt} \log R = p(s_1) - p(s_2). \tag{12c}$$

THEOREM 4. *In the above notation*

(i) $\lim S(t) = 0 \Leftrightarrow \lim X(t) = 0$.

(ii) *If* $b \leqslant a$ *then* $S(t)$ *and* $X(t)$ *have constant signs for* $t \gg 1$.

(iii) *If* $X(t)$ *and* $S(t)$ *have constant signs for* $t \gg 1$ *then* $\lim R(t)$ *exists and is positive and* $\lim S(t) = \lim X(t) = 0$.

(iv) *In any case,* $R(t)$ *and* $1/R(t)$ *are bounded.*

Proof of (i). Theorem 1 shows that S, S', X, X', X'' are all bounded, and boundedness of S'' is seen by differentiating (12a). Therefore Lemma 1 and (12a), (12b) give

$$\lim S(t) = 0 \Leftrightarrow \lim P(t) = 0 \Leftrightarrow \lim X(t) = 0.$$

Proof of (iii). If $S(t)$ does not change sign for $t > T$, as in the equation preceding (4), we get positive constants K, L such that

$$K(s_1 - s_2) \leqslant p(s_1) - p(s_2) \leqslant L(s_1 - s_2), \qquad t > T.$$

Hence by (12c),

$$KS \leqslant \frac{d}{dt} \ln R \leqslant LS. \tag{13}$$

If X also does not change sign for $t > T$, we will show that $R(t)$ is bounded above. Note that $S \leqslant 0 \Rightarrow R' \leqslant 0$ by (12c) and that $X \leqslant 0 \Rightarrow R \leqslant 1$. Hence the only case that needs consideration is that in which $S \geqslant 0$ and $X \geqslant 0$ for $t > T$. In this case $P \geqslant 0$ and (12a) give $aS \leqslant -S'$. Hence

$$a \int_{t_0}^{t} S(u)\, du \leqslant S(t_0) - S(t), \qquad t > t_0 > T.$$

Integrating (13) now shows that R is bounded above, and the same holds for $1/R$ by interchanging the roles of x_1 and x_2. Differentiating (12c), we see that R'' is bounded. When S has constant sign, R is monotone by (12c), so $\lim R(t) = A > 0$ exists. The Hadamard–Littlewood Theorem applied to $R(t) - A$ gives $\lim R'(t) = 0$, hence $\lim S(t) = 0$ by (12c) and $\lim X = 0$ by (i).

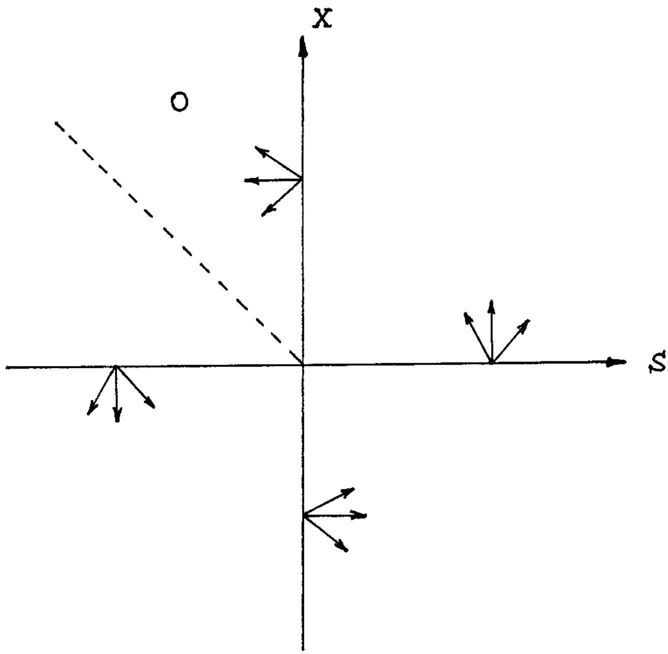

FIGURE 1

Proof of (iv). If the solutions are distinct, as now assumed, uniqueness of the solution (0, 0) ensures that the trajectory $S(t)$, $X(t)$ in the (S, X) plane does not go through the origin. By (12a), (12b)

$$X=0 \Rightarrow X' = x_1(p(s_1) - p(s_2)), \qquad S=0 \Rightarrow S' = -(x_1 - x_2)\, p(s_1).$$

Hence the direction field on the axes has the general character illustrated in Fig. 1. The trajectory either stays finally in a single quadrant or spirals around the origin in a counterclockwise direction. In the former case S and X are ultimately of constant sign and we have the conclusion (iii), which is stronger than (iv). In the latter case $R=1$ on the positive S axis and R increases to a maximum on the positive X axis before it returns to values $\leqslant 1$ in the lower half plane. (The maximum is on the X axis because $R' > 0$ when $S > 0$ and $R' < 0$ when $S < 0$.) The increase from the value of t at which $R=1$ to the value at which R is maximum can be estimated as in the proof of (iii) and shows that R is bounded above. That $1/R$ is bounded follows by interchanging x_1 and x_2.

Proof of (ii). If $b \leqslant a$ the equation $(S+X)' = -aS - bX$ gives

$$(X+S)' \geqslant -a(X+S) \qquad \text{when} \quad X \geqslant 0. \tag{14}$$

Hence if $X(t_0)+S(t_0)>0$ at some value t_0, and $X(t)\geqslant 0$ for $t\geqslant t_0$, then

$$X(t)+S(t)>ce^{-at}, \qquad t>t_0,$$

where c is a positive constant. In particular, this holds in the open angular region O bounded by the dotted line and the X axis in the figure. We have $X+S=0$ on the dotted line and $X+S>0$ in O. Hence (without leaving the half plane $X\geqslant 0$) a trajectory can never cross the dotted line from a point in O. The spiral behavior mentioned in connection with (iv) shows that if the trajectory does not ultimately stay in the first, third, or fourth quadrants, it can get into the second only by crossing the positive X axis. Since it cannot cross the dotted line, it must stay in O from then on.

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