

MONOTONE DYNAMICS OR NOT? DYNAMICAL CONSEQUENCES OF VARIOUS MECHANISMS FOR DELAYED LOGISTIC GROWTH

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Abstract. In this paper we interpret the global stability properties of the delayed single species chemostat in terms of monotone dynamics on an asymptotically invariant hyperplane in the state space. The consequence is a translation of advanced analysis and delay differential equations into sign checks and ordinary differential equations for an important single species model with explicit resource dynamics. Complete proofs are included, since the limiting behavior at asymptotically invariant sets may not agree with the limiting behavior of the original system even in the finite dimensional case (Thieme (1992)).

A delayed logistic equation based on explicit resource dynamics falls out as a limiting case of the chemostat and we claim this to be a new mechanistic interpretation of delayed logistic models. We continue by comparing these results to several other delayed logistic models that has been mechanistically justified in the literature. We conclude that monotone dynamics apply in several cases. We improve one global stability result that cannot be obtained with by the use of monotone dynamics and end up by pointing out the dynamical differences between Hutchinson's (1948) delayed logistic equation and those with mechanistic interpretations.

1. Introduction

In this paper we discuss the relation between the delayed chemostat

$$\begin{aligned} S'(T) &= CD - DS - \frac{AS(T)}{1 + ABS(T)}X(T), \\ X'(T) &= Me^{-DR} \frac{AS(T-R)}{1 + ABS(T-R)}X(T-R) - DX(T). \end{aligned} \quad (1)$$

and various forms of the delayed logistic equation that are going to be introduced later. Here, $S(T)$ is the substrate concentration at time T , $X(T)$ is the concentration of some organism at time T having the substrate S as its limiting resource. The parameters $C > 0$, $D > 0$, $A > 0$, $B > 0$, $M > 0$, $R > 0$ stand for concentration, dilution rate, search rate for the organism, handling time for the organism (cf. Holling (1959)), conversion factor for the organism, and time delay, respectively. The time delay could be included in many ways in the chemostat model, but we think that the above way is the most natural way to include it; in this way it takes into account that the organism cannot

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convert consumption of the substrate into own biomass instantaneously. Note the factor e^{-DR} , it corresponds to the fact that a part of the individuals that consume nutrient is washed out before they are able to reproduce.

The model above is a phenomenological model including the governing aspects of a number of ecological phenomena, cf. Smith and Waltman (1995). For instance, a lake ecology may have rivers transferring a limiting resource to the lake and rivers diluting this resource. Mechanistically, the key point of the chemostat model is its explicit modeling of the resource level and that all of its parameters can be interpreted in terms of either individual behavior or resource dynamics.

We start our analysis by re-parameterizing our model into a dimensionless form by the changes $t = DT$, $r = DR$, $s = S/C$, $x = X/C$, $a = AC/D$, $b = ABC$, and $m = M$. For simplicity, we introduce a function g defined by

$$g(s) = \frac{as}{1 + bs},$$

too. We note that g is strictly increasing with $g(0) = 0$. We arrive in the dimensionless form

$$\begin{aligned} \dot{s}(t) &= 1 - s(t) - g(s(t))x(t), \\ \dot{x}(t) &= me^{-r}g(s(t-r))x(t-r) - x(t) \end{aligned} \quad (2)$$

for which we impose the initial conditions $s(t) \geq 0$, $-r \leq t \leq 0$ and $x(t) \geq 0$, $-r \leq t < 0$, $x(0) > 0$. A number of important results regarding the model (2) has been proved and can be found in Smith (2011). They are that the solution space is $C([-r, 0], \mathbf{R}^2)$, solutions remain non-negative (Theorem 3.4), and bounded (Section 5.6). Either one or two equilibria, the washout state and the survival state exist, the washout state is globally attracting if it is the only equilibrium and so is the survival state if it exists (Theorem 5.16). The first proof of the global stability result can be found in Ellermeyer (1994). Thus, all global qualitative dynamical properties of the delayed single species chemostat model are known.

2. Methods

We list briefly the main methods that are going to be used in this paper. Most of this material can be found in the monographs of Hale and Lunel (1993), Smith (1995), and Smith (2011). We shall show that (2) reduces to a scalar equation on an invariant hyperplane, so we work throughout the paper with scalar autonomous delay differential equations of the form

$$\dot{x}(t) = f(x(t), x(t-r)) \quad (3)$$

satisfying an initial condition $x(t) = \phi(t)$, $-r \leq t \leq 0$. The solution of (3) starting at the initial condition $\phi \in C([-r, 0], \mathbf{R})$ is denoted by $x(t, \phi)$. We denote the right hand side by $f(x, y)$ when we want to refer to the different variables or take partial derivatives. Existence and uniqueness of the solutions of such equations are granted by the method of steps if f and f_x are continuous on \mathbf{R}^2 and ϕ is continuous on $-r \leq t \leq 0$ since the

equation becomes an ODE after substituting the continuous initial condition into the equation. Hence, standard ODE theory applies and grants existence and uniqueness of solutions of equations of form (3). It follows that the natural state space of the equation (3) is the continuous functions on the interval $-r \leq t \leq 0$, or $C([-r, 0], \mathbf{R})$.

The equations that we are going to consider arise in population dynamics and we are going to use a theorem granting that non-negative solutions remain non-negative. Such theorems require that solutions exist and are unique, but additional conditions are required. This additional condition is given by

$$f(0, y) \geq 0, \forall y \in \mathbf{R}_+ \tag{4}$$

and we note that this condition can be expressed in terms of the functions involved in the differential equation directly. Therefore, direct substitution in the involved expressions can be used to check these facts. Also this theorem is directly related to geometric ODE theory, it basically formulates conditions for when the vector field is either directed into the positive cone or along the boundaries of it. No problems arise when it is directed into the positive cone and in the latter case uniqueness of solutions grants that no solutions escape from the positive cone.

Studies of nonlinear ordinary differential equations usually start from analysis of equilibria. All equilibria can be found by neglecting delays and therefore they coincide with the equilibria of the corresponding ODE

$$\dot{x}(t) = f(x(t), x(t)). \tag{5}$$

We claim that we have found one equilibrium by solving $f(x, x) = 0$, say $x(t) = \bar{x}$. The linearization of (3) around the equilibrium \bar{x} is then given by

$$\dot{\xi}(t) = f_x(\bar{x}, \bar{x})\xi(t) + f_y(\bar{x}, \bar{x})\xi(t-r) = \alpha\xi(t) + \beta\xi(t-r). \tag{6}$$

We shall as usual look for exponential solutions around the zero solution of this equation and these are characterized by the characteristic equation

$$\lambda = \alpha + \beta e^{-\lambda r}. \tag{7}$$

The solutions of (7) classifies the solutions of (6) into four cases according to the following theorem (Theorem 4.7 in Smith (2011)):

THEOREM 1. *The following hold for (6).*

- (A) *If $\alpha + \beta > 0$, then $\xi = 0$ is unstable*
- (B) *If $\alpha + \beta < 0$, $\beta \geq \alpha$, then $\xi = 0$ is asymptotically stable regardless of the magnitude of the delay.*
- (C) *If $\alpha + \beta < 0$, $\beta < \alpha$, then there exist threshold value for the delay r_* such that $\xi = 0$ is asymptotically stable for $0 < r < r_*$ and unstable for $r > r_*$. The value r_* can be explicitly computed and is given by*

$$r_* = \frac{\arccos\left(-\frac{\alpha}{\beta}\right)}{\sqrt{\beta^2 - \alpha^2}} \tag{8}$$

(D) If $\alpha + \beta = 0$, then $\lambda = 0$ is a root of (7).

In cases (D) and (C) with $r = r_*$, the linearization (6) does not provide the qualitative information requested regarding solutions of the original nonlinear equation (3) in the vicinity of its equilibrium \bar{x} . However, center manifold theory exist in the delay differential equation case (e. g. Diekmann, van Gils, Verduyn Lunel, and Walther (1995)). Consequently, formulas like the Hopf-bifurcation stability formula (formula (3.4.11) in Guckenheimer and Holmes (1983)) could be developed in this case, too.

In ODE theory there exists a standard method for constructing Lyapunov functions for linear equations when all characteristic roots have negative real part, see Jordan and Smith (1990). There are extensions of this method to delay equations, see Hale and Lunel (1993), but in most cases explicit constructions can be very complicated already in simple cases and most results exist just in the case (B) above. To get Lyapunov functions that are valid for the nonlinear equations like (3), such results still usually need to be modified.

The method of Lyapunov functions and LaSalle's (1960) invariance principle is always the most desirable when proving global stability. However, more straightforward methods might exist. We start by mentioning the following simple comparison theorem (Smith (2011), Theorem 3.6). Essentially, it states that if a solution start in front of (behind) another and grows faster (slower), it will stay in front of (behind) the other.

THEOREM 2. Consider (3) and suppose that f and f_x are continuous on \mathbf{R}^3 and that the initial condition ϕ is continuous on $[-r, 0]$. Let $x(t)$ be a solution of (3) with $x(t) = \phi(t)$ for $[-r, 0]$ on some interval $[0, \hat{s}]$, $\hat{s} > 0$. Let $\bar{x}(t)$ be continuous on $[-r, 0] \cup [0, \hat{s}]$, differentiable on $[0, \hat{s}]$ and satisfy

$$\begin{aligned}\dot{\bar{x}}(t) &\geq (\leq) f(\bar{x}(t), \bar{x}(t-r)), t \in [0, \hat{s}], \\ \bar{x}(t) &\geq (\leq) \phi(t), -r \leq t \leq 0.\end{aligned}$$

Then $\bar{x}(t) \geq (\leq) x(t)$.

We continue formulating conditions that preserve the order of two solutions as follows. It is Theorem 5.9 in Smith (2011).

THEOREM 3. Consider (3). Assume that $f : \mathbf{R}^2 \rightarrow \mathbf{R}$, f_x , f_y are continuous, $f_y(x, y) \geq 0$, and that $x_1(t)$ and $x_2(t)$ are two solutions of (3) defined on $[-r, \hat{s}]$, for some \hat{s} . If $x_1(t) \leq x_2(t)$ for $t \in [-r, 0]$, then $x_1(t) \leq x_2(t)$ for $t \in [-r, \hat{s}]$.

This theorem is a direct consequence of the previous theorem and makes it possible to translate many of the properties of the equilibria of the scalar ordinary differential equation (5) to (3). The following theorem contains the parts of Corollary 5.11 in Smith (2011) that we shall need.

THEOREM 4. Consider (3). Assume that $f : \mathbf{R}^2 \rightarrow \mathbf{R}$, f_x , f_y are continuous, $f_y(x, y) \geq 0$. Let $\bar{x} \in (\underline{m}, \bar{m})$ be an equilibrium of (5), and hence of (3). Suppose that the sign-condition

$$(x - \bar{x})f(x, x) < 0, x \in [\underline{m}, \bar{m}], x \neq \bar{x}$$

holds. If $\phi(s) \in [\underline{m}, \overline{m}]$, $s \in [-r, 0]$, then

$$\lim_{t \rightarrow \infty} x(t, \phi) = \bar{x}.$$

3. A delayed hyperbolic model

A relation between the single species chemostat model and the logistic model exists, see e. g. Kooi, Boer, Kooijman (1998) and this relation can be made visible also in the delayed case. More precisely, the logistic equation can be considered as an approximation of the mass-balance equations used in the chemostat. Let us consider the functional

$$V(t) = x(t) + me^{-r}s(t-r) - me^{-r}. \tag{9}$$

Along the solutions of (2), we identify that the equation for the total derivative is the ordinary differential equation $\dot{V}(t) = -V(t)$ and thus, $\lim_{t \rightarrow \infty} V(t) = 0$. We ask what models we could obtain by considering the delayed chemostat in the hyperplane $V = 0$ in $C([-r, 0], \mathbf{R}^2)$. It is not evident that such a procedure will preserve limit sets even in the finite dimensional case (Thieme (1992)) but we try this substitution and get

$$\dot{x}(t) = me^{-r}g\left(\frac{me^{-r} - x(t)}{me^{-r}}\right)x(t-r) - x(t). \tag{10}$$

This is a single hyperbolic delayed equation. Our program is for the moment to verify that this equation inherits the qualitative dynamical properties of the single species chemostat model. Indeed, we prove the following sequence of results.

LEMMA 1. *Solutions of (10) remain non-negative and bounded above by $x(t) < me^{-r}$.*

Proof. We start by proving that the solutions remain non-negative. This follows from the fact that (4) takes the form

$$me^{-r}g(1)x(t-r) \geq 0$$

and this condition holds for all positive $x(t-r)$. Comparison with

$$\dot{x}(t) \leq -x(t)$$

for $x(t) \geq me^{-r}$ shows that large positive solutions decay at least exponentially since $g(s) < 0$ for $s < 0$. It follows that positive solutions are bounded above by $x(t) < me^{-r}$. □

LEMMA 2. *The equation (10) has the washout state $x = 0$ as its unique non-negative equilibrium if $g(1) < \frac{e^r}{m}$. This equilibrium is then locally stable. If $g(1) > \frac{e^r}{m}$, then (10) has two non-negative equilibria, the washout state that is locally unstable and the survival state that is locally stable.*

Proof. By neglecting delays, we get that the washout state is an equilibrium. For the survival state we solve

$$g\left(\frac{me^{-r} - x(t)}{me^{-r}}\right) = \frac{e^r}{m}$$

and conclude that this equation has a unique positive solution $x(t) = \bar{x}$ if and only if $g(1) > \frac{e^r}{m}$. In order to investigate the local stability of these solutions, we compute the characteristic equation of a generic equilibrium of the equation (10). It takes the form

$$\lambda + 1 + xg'(s) - e^{-\lambda r}me^{-r}g(s) = 0$$

that turns out to be the second factor of the characteristic equation of the delayed single species chemostat (2), see Smith (2011, p55). The factorization of this equation given there is therefore, not a coincidence. It is closely related to motion in the hyperplane $V = 0$ defined by (9) and motion towards it. Hence, we have proved that the local stability properties of the delayed single species chemostat (2) and the hyperbolic model (10) are the same. \square

We go on formulating the global properties of (10) and remark that we use the monotone dynamics of it in order to arrive in the conclusions. This is a simplification in comparison to proving the global stability properties of the chemostat equations (2) directly, since the first equation does not satisfy the quasimonotone condition in Smith (2005). Up our knowledge, the possibilities for using monotone dynamics in order to arrive in the global stability conclusions for the chemostat has not been pointed out in the literature before. In particular, they have not been mentioned in textbooks aiming at elementary presentations of the use of delay equations in the life sciences (Smith (2011)).

THEOREM 5. *The following statements hold for the solutions of (10).*

- (i) *If $g(1) < \frac{e^r}{m}$, then the washout equilibrium is the unique non-negative equilibrium of (10) and it attracts all non-negative solutions.*
- (ii) *If $g(1) > \frac{e^r}{m}$, then the survival equilibrium exists for (10) and it attracts all positive solutions.*

Proof. Consider (10). By Lemma 1, we have $0 \leq x(t) < me^{-r}$. With aid of the differential inequality

$$\dot{x}(t) \leq me^{-r}g(1)x(t-1) - x(t)$$

we notice that no solutions can grow faster than the solutions of the linear delay differential equation

$$\dot{z}(t) = me^{-r}g(1)z(t-1) - z(t) \tag{11}$$

which has the characteristic equation $\lambda = -1 + me^{-r}g(1)e^{-\lambda}$. Now

$$me^{-r}g(1) < 1 \tag{12}$$

implies that the zero solution of (11) is asymptotically stable and falls into category (B) of Theorem 1. Therefore, all solutions of (10) converge to zero if (12) since they are bounded from above by solutions that decay to the zero solution.

Now assume $me^{-r}g(1) > 1$ and remember that $x(0) > 0$. The differential inequality $\dot{x}(t) > -x(t)$ gives $x(t) > 0$. We can therefore, work with initial conditions satisfying $x(t) \geq \underline{m}$, for some $\underline{m} > 0$ and $-r \leq t \leq 0$. Consider (10). It possesses monotone dynamics (or order-preserving dynamics, see Smith (1995)) since $0 \leq x(t) \leq me^{-r}$ gives

$$me^{-r}g\left(\frac{me^{-r} - x(t)}{me^{-r}}\right) \geq 0$$

so that Theorem 3 can be applied. Consider the non-negative equilibria of (10) that are 0 and \bar{x} when $me^{-r}g(1) > 1$. Both equilibria are shared with the ODE

$$\dot{x}(t) = \left(me^{-r}g\left(\frac{me^{-r} - x(t)}{me^{-r}}\right) - 1 \right) x(t).$$

For this ODE, the survival state is globally asymptotically stable on $x(t) \in (0, me^{-r})$. Theorem 4 gives that $x(t) = \bar{x}$ attracts all solutions of (10) with initial conditions satisfying $0 < \underline{m} \leq x(t) \leq \bar{m} < me^{-r}$. In the beginning of this proof and in the proof of Lemma 1 we have justified that we can work with such initial conditions provided $x(0) > 0$ and $x(t) \geq 0$ for $-r \leq t < 0$. Note that $x(t)$ remains continuous on any interval and thus, attains its maximum and minimum at some closed interval (Rudin(1987)), in this case $[\underline{m}, \bar{m}]$. □

Thus, the delayed hyperbolic model (10) preserves the dynamics of the delayed single species chemostat model (2). We conclude that $b = 0$ gives $g(s) = as$. Thus, the delayed logistic model

$$\dot{x}(t) = ame^{-r}x(t-r) - x(t) - ax(t)x(t-r) \tag{13}$$

shares the dynamical properties. In particular, we conclude that it has monotone dynamics when $0 \leq x(t) \leq me^{-r}$. If we let the delay parameter tend to zero, this equation becomes the ordinary differential equation

$$\dot{x}(t) = (am - 1)x(t) - ax^2(t) = (am - 1)x(t) \left(1 - \frac{x(t)}{\frac{am-1}{a}} \right).$$

Here we can identify the growth rate and carrying capacity parameters as $am - 1$ and $(am - 1)/a$, respectively. The washout equilibrium is still given by $x(t) = 0$ and the survival equilibrium is located at the carrying capacity $x(t) = (am - 1)/a$.

4. Other mechanisms for logistic growth

Assuming constant resources, Geritz and Kisdi (2012) argued for two very similar delayed logistic models. The first model stands for site-competition and both models

have a delay between egg-laying and hatching. None of them have the explicitly described resource dynamics as described by the chemostat. Their model is similar to the model studied by Cooke (1979) in an epidemiological context and takes the form

$$\dot{X}(T) = MX(T - R) \left(1 - \frac{X(T)}{K} \right) - DX(T).$$

After the scaling $t = DT$, $r = DR$, $m = M/D$, and $x = X/K$, it takes the form

$$\dot{x}(t) = mx(t - r)(1 - x(t)) - x(t).$$

This equation is a special case of (13) and therefore, we conclude that it has the same properties including the important monotonicity and global stability properties for $m > 0$ and $0 \leq x(t) \leq 1$. In Cooke (1979) similar global results were obtained by the use of Lyapunov functions (Hale and Lunel(1993)).

We continue with a possible variation of this model. Liz (2014) considered the model

$$\dot{X}(T) = MX(T - R) \max\left(1 - \frac{X(T - R)}{K}, 0\right) - DX(T).$$

Constant resources are used here, too. The difference is that the limiting resource limits the number of eggs and not the adult egg-laying behavior. The maximum is taken in order to ensure that non-negative solutions remain non-negative. Also here, we can do the scaling $t = DT$, $r = DR$, $m = M/D$, and $x = X/K$ and obtain

$$\dot{x}(t) = mx(t - r) \max(1 - x(t - r), 0) - x(t) \tag{14}$$

The monotonicity arguments do not apply here, so the suggested change results in more complicated dynamics. The dynamics of the model is interesting and it constitutes a link between the discrete logistic model (Devaney (1989)) and Verhulst (1938) logistic model. The washout equilibrium $x = 0$ exists for $m \geq 0$. An additional survival equilibrium $\bar{x} = 1 - (1/m)$ exist for $m > 1$. The positive equilibrium is locally asymptotically stable if either $1 < m \leq 3$, or $m > 3$ and

$$0 < r < r_* = \frac{\arccos\left(\frac{1}{2-m}\right)}{\sqrt{(m-1)(m-3)}}.$$

The thresholds above follow directly from Theorem 1 and (8) since the linearization of (14) in the vicinity of \bar{x} is given by

$$\dot{\xi}(t) = -\xi(t) + (2 - m)\xi(t - r).$$

One remarkable result in Liz (2014) is anyway the global stability result. It is based on results that use the limit the number of possible attractors for negative Schwartzian discrete maps (Singer (1978)). Such results can then be used to provide bounds for the number of attractors for delay differential equations (Györi and Trofimchuk (1999) and Liz and Röst (2010)). It states that \bar{x} is globally asymptotically stable if either $1 < m \leq 3$, or $3 < m < 4$ and

$$0 < r < \ln\left(\frac{m-2}{m-3}\right).$$

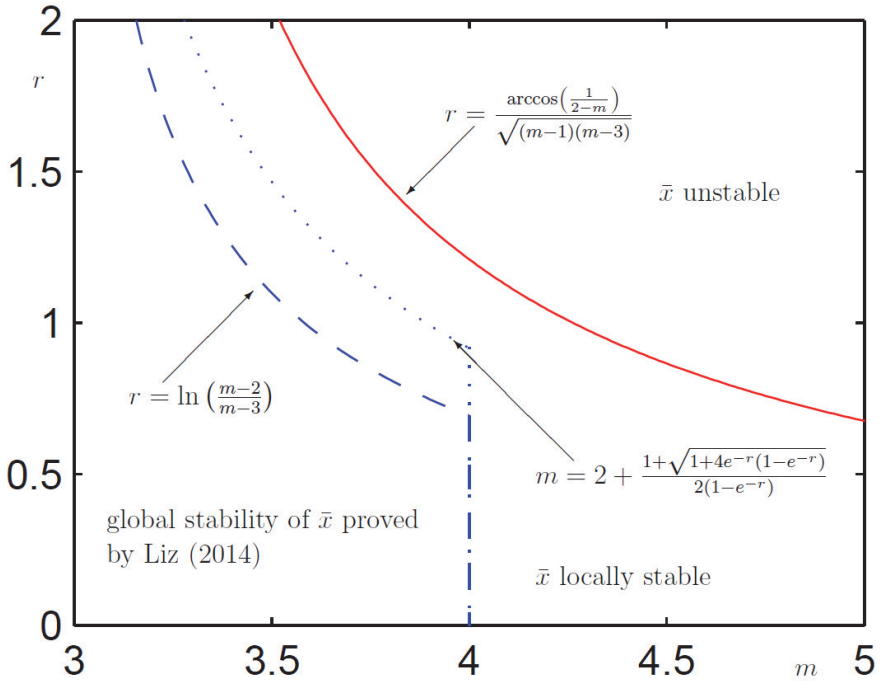


Figure 1: Bifurcation diagram of (14) including the area with proved global stability according to Liz (2014). We add an additional area of global stability as indicated between the dashed and the dotted lines.

Figure 1 relates the areas of local stability with the areas where global stability is confirmed. These results can still be improved. Application of Corollary 16 in Györi and Trofimchuk (1999) gives the global stability condition $3 < m < 4$ and

$$m < 2 + \frac{1 + \sqrt{1 + 4e^{-r}(1 - e^{-r})}}{2(1 - e^{-r})}.$$

This adds an area of global stability that we have displayed between the dashed and dotted lines in Figure 1. Our scaling above makes it possible to include all these results in planar bifurcation diagrams.

Another way to end up in a different delayed logistic equation according to Geritz and Kisdi (2012) is inference competition. Then the model takes the form

$$\dot{X}(T) = MX(T - R) - DX(T) - FX^2(T). \tag{15}$$

Also here, we introduce the scaling $t = DT$, $r = DR$, $x = \frac{F}{M}X$, $m = M/D$ and end up with

$$\dot{x} = mx(t - r) - x(t) - mx^2(t).$$

This model has different structure and cannot be obtained by selecting parameters in (13). The monotonicity condition is nevertheless satisfied for $m > 0$. Neglecting delays gives the equilibria $x(t) = 0$ and $x(t) = \frac{m-1}{m}$ and one of these equilibria is locally stable. By Theorem 4, the locally stable equilibrium attracts all positive initial conditions.

We continue with the alternative delayed logistic model given by Arino, Wang, and Wolkowicz (2006). It takes the form

$$\dot{X}(T) = \frac{MDX(T - R)}{De^{DR} + F(e^{DR} - 1)X(T - R)} - DX(T) - FX^2(T) \tag{16}$$

and here the growth rate is assumed proportional to the number of individuals in the population $T - R$ time units in the past still alive at time T . In their paper, there is no explicit individual behavior linked to integrated death rate accounting for the terms

$$\dot{X}(T) = -DX(T) - FX^2(T).$$

There are possibilities for interpreting this term as lethal encounters (Geritz and Kisdi (2012)) as in (15). Also here, the number of parameters can be reduced by the use of the scaling $t = DT$, $r = DR$, $x = \frac{F}{M}X$, $m = M/D$ resulting in

$$\dot{x}(t) = \frac{mx(t-r)}{e^r + m(e^r - 1)x(t-r)} - x(t) - mx^2(t).$$

Results including monotone dynamics and convergence of solutions towards equilibria for (16) are formulated in Arino, Wang, and Wolkowicz (2006). We remark that all models in this section assume static resources.

5. The classical delayed logistic equation

Delayed logistic equations are not always derived in a way that preserves the dynamical properties of the underlying chemostat equations. Consider, for instance, Hutchinson’s (1948) delayed logistic model

$$\dot{x}(t) = (am - 1)x(t) \left(1 - \frac{x(t-r)}{a} \right). \tag{17}$$

We remind the reader that the resource dynamics was not modeled explicitly in Hutchinson’s paper and that the problems mentioned by Kooi, Boer, Kooijman (1998) exist. Nisbet and Gurney (1982) list several serious flaws of this model in a population dynamical context including not clearly defined birth- and death processes. They continue by clearly pointing out the insufficiency of this model for explaining data in the Nicholson (1954,1957) blowfly case. This equation can be made comparable to (13) by arranging it as

$$\dot{x}(t) = am \cdot x(t) - x(t) - ax(t)x(t-r).$$

We note that the above equation has preserved the equilibria at $x(t) = 0$ and $x(t) = (am - 1)/a$. However, it does not have monotone (order-preserving) solutions, since

$$-ax(t) \leq 0. \tag{18}$$

We start by linearizing around a generic equilibrium x and get the characteristic equation

$$\lambda = (am - 1 - ax) - e^{-r\lambda}ax.$$

For $x(t) = 0$, we have $\lambda = am - 1$ and for $x(t) = (am - 1)/a$, we have

$$\lambda = -e^{-r\lambda}(am - 1)$$

which according to Theorem 1 belong to the category (C) above: There exists a Hopf-bifurcation value for the magnitude of the delay, so that the equilibrium is stable if the delay is below that threshold and unstable otherwise.

In order to investigate (17) further, we introduce $\tau = t/r$, $\mu = (am - 1)r$ and

$$\xi = \frac{x}{\frac{am-1}{a}} - 1.$$

We get

$$\frac{d\xi(\tau)}{d\tau} = -\mu\xi(\tau - 1)(1 + \xi(t)), \tag{19}$$

which is the famous Wright’s (1955) equation. We limit our consideration to solutions that correspond to positive solutions of (17), ie $-1 < \xi < \infty$.

The following is known about (19). First, all solutions are bounded (Proposition 5.13 in Smith (2011)). Wright (1955) proved global stability of the zero solution for $0 \leq \mu \leq \frac{3}{2}$ and mentioned that his methods can be used for proving global stability in the range $0 \leq \mu \leq \frac{37}{24}$ and probably to $0 \leq \mu \leq 1.567$. Wright’s (1955) conjecture claims global stability to hold for all values of the delay in the range $0 \leq \mu \leq \frac{\pi}{2}$ and this conjecture has been an open problem since it was formulated. The last improvement of the above result is that for $0 \leq \mu \leq 1.5706$, then every orbit tends to the zero solution (Bánheley, Czendes, Kristin, and Neymaier (2014)). Note that $1.5706 < \frac{\pi}{2} \approx 1.5707963268$.

Wright’s (1955) global stability result for the zero solution for $0 \leq \mu \leq \frac{3}{2}$ has been subject of some other generalizations, too, often called 3/2-conditions. Such generalizations often involve non-constant values for the growth rate parameter μ , see e. g. Faria (2004), Kuang (1993), So and Yu (1995). Further, Gopalsamy (1992) formulated a number of global stability theorems for related models with delays.

There exists at least one periodic solution for (19) when $\mu > \frac{\pi}{2}$. There are theorems that limit the complexity of the dynamics of (19). For instance, uniqueness of slowly oscillating solutions has been proved (Xie(1993)). Inequality (18) excludes more complicated behavior than periodic solutions (Mallet-Paret and Sell (1996)).

We can therefore ask whether it is always a simplification to use logistic equations instead of the chemostat when modeling the growth rate of the lowest trophic level. The single-species delayed chemostat has a complete qualitative analysis but this is far from the case with all variants of the delayed logistic equation.

6. Summary

In this paper we have studied a delayed model for the single species chemostat. The global dynamics of this model has been completely known since Ellermeyer (1994). The analysis has been improved since then (Smith(2011)). All solutions tend to either the washout or the survival state and the local stability properties of those equilibria fully determine the global properties of the model.

We make a new interpretation of these results here. The results can be divided into motion towards a hyperplane in $C([-r, 0], \mathbf{R}^2)$ and motion in the hyperplane governed by a scalar monotone delay differential equation. We name this equation, the hyperbolic model. Such a separation is not always valid for limit sets even in the finite dimensional case (Thieme (1992)). The question is whether such a method can be validated for more general invariant sets, like chain-recurrent sets (Conley (1978) and Hirsch, Smith, and Zhao (2001)). We verify that no qualitative differences occur between the chemostat equations and the hyperbolic model. In conclusion, the reason for that the chemostat model is completely known is that it is asymptotically equivalent to a monotone dynamical system, our hyperbolic model. This is evident both in the proofs of the local properties as it is in the proofs of the global properties.

A limiting case of this hyperbolic model corresponds to a delayed logistic model. We prove that the delayed logistic growth rate model encountered in this way agrees dynamically with several other mechanistically justified delayed logistic models (Arino, Wang, and Wolkowicz (2006), Cooke (1979), Geritz and Kisdi (2012)). None of these possess an explicit description of the resource dynamics as is the case with the logistic model as derived as a limiting case of the chemostat. Some variants of these models cannot be analyzed by the use of monotone dynamics and possess therefore more complicated dynamics (Liz (2014)). We add a non-trivial region possessing proved global stability to one of these models here.

However, none of these models do correspond to the model that usually is referred to as the classical delayed logistic model in the literature (Hutchinson (1948)). This model does not satisfy any monotonicity conditions (Smith (1995)) and is equipped with a number of problems regarding its long-run dynamical behavior that has been open for a long time, see Bánheley, Czendes, Kristin, and Neymaier (2014). However, despite its unclear links to mechanistically formulated models, it has motivated a substantial amount of research and will probably do so in the future, too.

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