Application of Delay Equations

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Let $N(t)$ be the size of the total population at time t and let $\dot{N}(t) = dN/dt$ be its rate of growth.
The *per capita rate of growth* of the population at time t is

$$\frac{\dot{N}(t)}{N(t)}.$$

(It is the rate of growth devided by the total population size.)
The simplest model leads to the equation

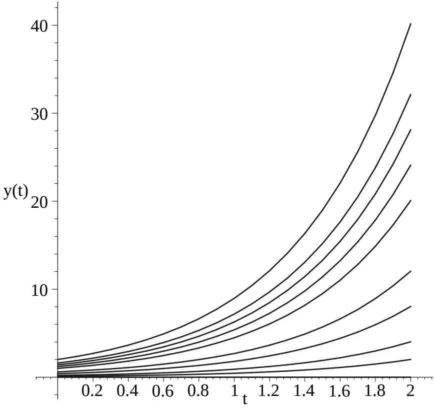
$$\frac{\dot{N}(t)}{N(t)} = r, \qquad \text{or} \qquad \dot{N}(t) = rN, \tag{1}$$

where $r > 0$ is a constant.
The initial condition:

$$N(0) = N_0 \qquad (N_0 > 0). \tag{2}$$

This is the model for exponential growth since the solution of (1)-(2) is

$$N(t) = N_0 e^{rt}, \qquad t \geq 0.$$



$r = 2$

(i) One would expect pure exponential growth when there is unlimited space and resources.

(ii) The per capita rate of growth should depend on the population size.

So the model should be of the form

$$\frac{\dot{N}(t)}{N(t)} = f(N(t)) \qquad \text{or} \qquad \dot{N} = Nf(N)$$

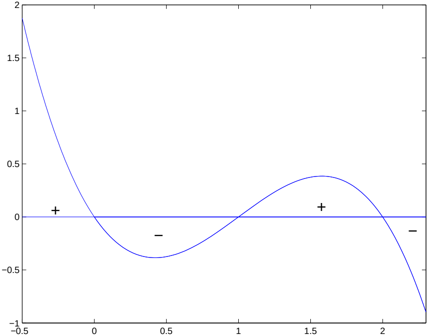
where the task is to select a plausible function f for the investigated problem.

A possible set of principles which might guide the selection of $f(x)$ are:

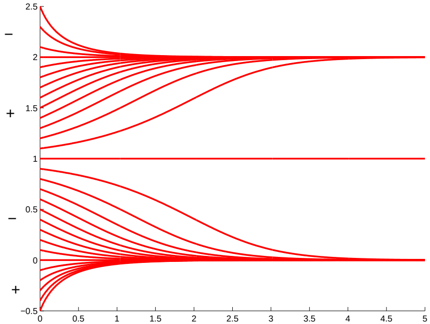
(1) When the population size is small, its growth is locally exponential. So $f(x) > 0$ for all $x \geq 0$ small enough.

(2) Too large population inhibits the rate of growth and hence $f(x)$ should be negative for all x large enough.

(3) The per capita rate should decrease as the population increases and the size is large enough. So $f(x_1) < f(x_2)$, $A \leq x_2 < x_1$, where $A \geq 0$ is fixed.



$$f(x) = x(x-1)(2-x)$$



$$N'(t) = N(t)(N(t)-1)(2-N(t))$$

The most frequently used forms of f and the related equations:

(a) The simplest function satisfying condition (1)-(3) is a linear one:

$$f(x) = r - mx, \qquad x \geq 0; \qquad r, m > 0 \quad \text{are given.}$$

Then

1. $f(x) > 0$ for $x < \frac{r}{m}$.
2. $f(x) < 0$ for $x > \frac{r}{m}$.
3. $f'(x) = -m < 0$.

The related differential equation:

$$\dot{N} = N(r - mN), \quad N(0) = N_0; \quad r, m, N_0 > 0.$$

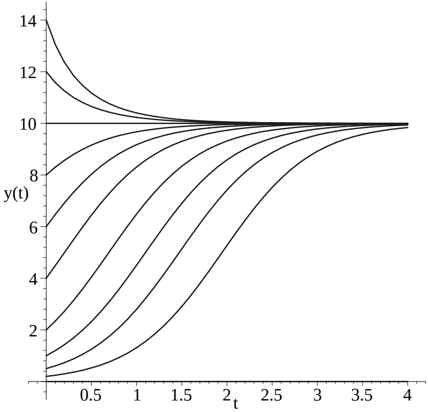
Letting $K = \frac{r}{m}$, we get

$$\dot{N} = rN\left(1 - \frac{N}{K}\right), \quad N(0) = N_0; \quad r, m, N_0 > 0. \qquad (3)$$

K is called the *carrying capacity* (or optimal size) of the population.

Eq. (3) is called *logistic equation*. Its solution is the so-called logistic curve

$$N(t) = \frac{KN_0}{N_0 + (K - N_0)e^{-rt}}, \qquad t \geq 0.$$



$r = 2,\ m = \frac{1}{5}$

The logistic equation has been used successfully to modell the growth of yeast cells, fruit flies, the population of Sweden and USA, the Pacific Halibut fishery and so on.

Two models for the harvesting of a population with logistic growth:

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - H,$$

where $H > 0$ is the constant harvesting rate (hunting, fishing, or a disease). Then

$$g(N) = \begin{cases} -\frac{r}{K}(N - N_1)(N - N_2), & H < \frac{rK}{4}, \\ -\frac{r}{K}\left(N - \frac{K}{2}\right)^2, & H = \frac{rK}{4}, \\ -\frac{r}{K}\left[\left(N - \frac{K}{2}\right)^2 + K\left(\frac{H}{r} - \frac{K}{4}\right)\right], & H > \frac{rK}{4} \end{cases}$$

where

$$K > N_1 := \frac{K + \sqrt{K(K - 4H/r)}}{2} > N_2 := \frac{K - \sqrt{K(K - 4H/r)}}{2} > 0.$$

$$\dot{N} = rN\left(1 - \frac{N}{K}\right) - hN,$$

where $h > 0$ hN is the harvesting rate, and

$$g(N) = -\frac{r}{K}N\left(N - \left(1 - \frac{h}{r}\right)K\right).$$

(b) *Gompertz equation*

$$\dot{N} = rN \ln\left(\frac{K}{N}\right); \qquad r, K > 0 \ \text{ constants.}$$

Here $f(x) = r\ln\left(\frac{K}{x}\right), \quad x > 0.$
Letting $x(t) = \ln N(t), \quad t > 0.$ Then

$$\dot{x}(t) = r\ln K - rx(t), \qquad t \geq 0.$$

Applied to the study of animal tumors.

(c) $\dot{N} = \frac{rN(K-N)}{K+\varepsilon N}$, where $\varepsilon > 0$ is small.

(d) $\dot{N} = rN\left(1 - \left(\frac{N}{K}\right)^{\alpha}\right)$, where $\alpha > 0$ is constant.

The above equations give the models of population growth in self regulated case when f is not constant. The regulation is instantaneous since the per capita rate at time t depends on the size of the population at the same time t.

The per capita rate at time t is equal to a function of the population size not only at time t but also at some earlier time.
Let us consider only the basic logistic equation. In that case the simplest model leads to the equation

$$\frac{\dot{N}(t)}{N(t)} = r - mN(t-\tau), \qquad t \geq 0,$$

where $r, m > 0$ and $\tau > 0$ are given constants. The constant τ is called delay or time lag. (In fact, it might be considered as the reaction time of the system.) So the simplest delayed logistic equation is as follows

$$\dot{N}(t) = N(t)\left(r - mN(t-\tau)\right), \qquad t \geq 0, \tag{4}$$

or equivalently

$$\dot{N}(t) = rN(t)\left(1 - \frac{N(t-\tau)}{K}\right), \qquad t \geq 0; \quad K = \frac{r}{m}. \tag{5}$$

The derivation of of (4) was given by Hutchinson (1948) and an other way by Cunningham (1954).

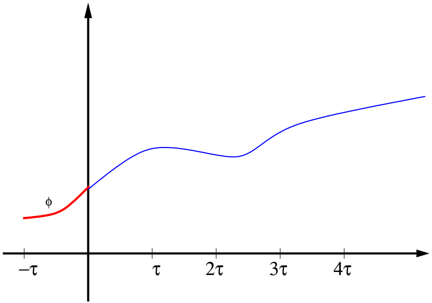
The initial condition is

$$N(t) = \varphi(t), \qquad -\tau \leq t \leq 0, \tag{6}$$

where $\varphi \in C\left([-\tau, 0], [0, \infty)\right).$

Solution of problem (4)-(6) can be given by using the so-called "step by step" method. Namely if $\tau > 0$ and $t \in [0, \tau]$, then $t - \tau \in [-\tau, 0]$ and hence

$$N(t - \tau) = \varphi(t - \tau)$$



Method of steps

Thus

$$\dot{N}(t) = rN(t)\left(1 - \frac{\varphi(t-\tau)}{K}\right), \qquad t \geq 0,$$

and hence

$$N(t) = N_1(t), \qquad 0 \leq t \leq \tau,$$

where

$$N_1(t) = \varphi(0)\exp\left(\int_0^t r\left(1 - \frac{\varphi(s-\tau)}{K}\right)\right) ds, \qquad 0 \leq t \leq \tau.$$

In general

$$N(t) = N_n(t), \qquad (n-1)\tau \leq t \leq n\tau, \qquad n \geqq 1,$$

where

$$N_n(t) = N_{n-1}((n-1)\tau)\exp\left(\int_{(n-1)\tau}^t r\left(1 - \frac{N_{n-1}(s-\tau)}{K}\right)\right) ds,$$

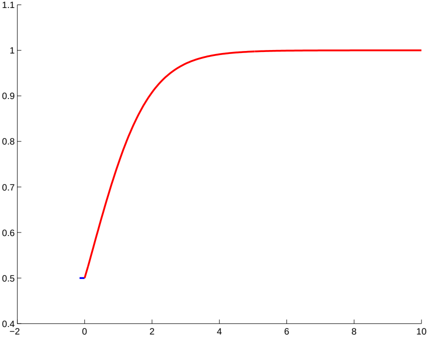
for $(n-1)\,\tau \leq t \leq n\tau, \quad n \geqq 1.$
The sequence of functions $N_n : [(n-1)\,\tau, n\tau] \longrightarrow \mathbb{R}$ is well-defined, and the function $N : [0, \infty) \longrightarrow \mathbb{R}$ defined by

$$N(t) = N_n(t), \qquad (n-1)\tau \leq t \leq n\tau, \qquad n \geqq 1,$$

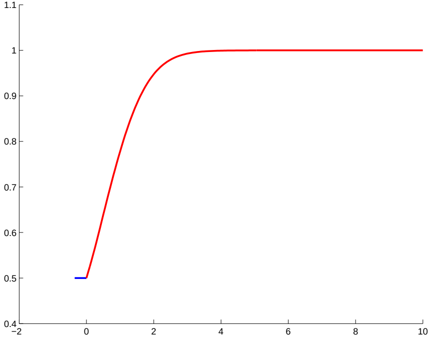
is the unique solution of the delayed logistic equation (4) with initial condition (6).
Now consider a special case of (4) with the parameter values:

$$r = 1, \qquad m = 1 \qquad \text{and} \qquad \varphi(t) = 0.5, \qquad -\tau \leq t \leq 0,$$

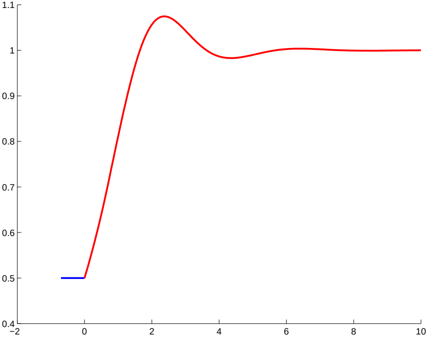
where $\tau \geq 0$ is an arbitrarily fixed parameter.
Let us consider the cases:



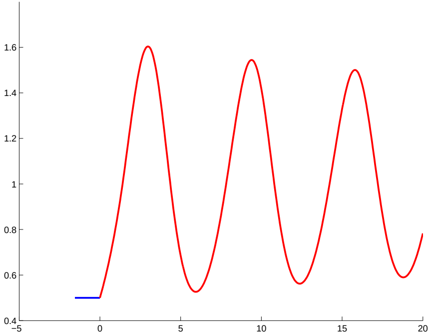
$\tau = 1/2e$



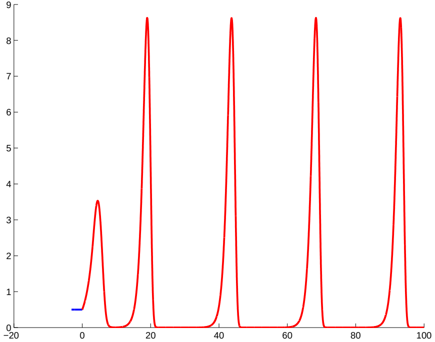
$\tau = 1/e$



$\tau = 2/e$



$\tau = \pi/2$



$$\tau = \pi$$

$$\dot{N}(t) = N(t)\left(r - mN(t-\tau)\right), \qquad t \geq 0, \tag{4}$$

Transformations of Eq. (4):

(1) Change the time scale (Kakutian and Markus (1958).
Let $y : [-1, \infty) \to \mathbb{R}_+$ be defined by

$$y(t) = N(\tau t), \qquad t \geq -1,$$

where $N : [-\tau, \infty) \to \mathbb{R}_+$ is the solution of (4). Then

$$\dot{y}(t) = \tau \dot{N}(\tau t) = r\tau N(\tau t)\left(1 - \frac{N(\tau t - \tau)}{K}\right),$$

and hence

$$\dot{y}(t) = r\tau y(t)\left(1 - \frac{y(t-1)}{K}\right), \qquad t \geq 0.$$

$$\dot{N}(t) = N(t)\left(r - mN(t-\tau)\right), \qquad t \geq 0, \tag{4}$$

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(2) Wright's transformation (1955).
Let

$$y(t) = \frac{N(\tau t)}{K} - 1, \qquad t \geq -1.$$

Then

$$\dot{y}(t) = -r\tau(1 + y(t))y(t-1) \qquad \text{Wright equation}$$

$$\dot{N}(t) = N(t)\left(r - mN(t-\tau)\right), \qquad t \geq 0, \tag{4}$$

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(3) Logarithmic transformation

Since the solution $N(t)$ is positive whenever $\varphi(t) > 0, \;\; -\tau \leq t \leq 0,$ the function

$$x(t) = \ln \frac{N(t)}{K} \qquad t \geq -\tau,$$

is well defined, where $K = \frac{r}{m}$. Clearly, $N(t) = Ke^{x(t)}, \;\; t \geq -\tau.$
Then

$$\dot{x}(t) = \frac{\dot{N}(t)}{N(t)} = r - mN(t-\tau) = r - re^{x(t-\tau)}, \qquad t \geq -\tau.$$

So problem (4)-(6) is equivalent to the problem

$$\dot{x}(t) = r(1 - e^{x(t-\tau)}), \qquad t \geq 0, \tag{7}$$

and

$$x(t) = \ln \varphi(t), \qquad -\tau \leq t \leq 0. \tag{8}$$

Eq. (7) is a delay differential equation, where the initial function $\ln \varphi(t)$ is continuous on $[-\tau, 0]$, but it is not necessarily positive (in general it is not positive).
Clearly

$$x(t) > 0 \Longleftrightarrow N(t) > K$$

$$x(t) = 0 \Longleftrightarrow N(t) = K$$

and

$$x(t) < 0 \Longleftrightarrow N(t) < K.$$

So N is oscillatory (nonoscillatory) about K if and only if x is oscillatory (nonoscillatory) about zero. The solution N tends to K as $t \to +\infty$ if and only if x tends to 0 as $t \to +\infty$.
This means that the optimal size K atracts the solutions of Eq. (4) if the zero atracts the solutions of Eq. (7) at infinity.
It is clear that $N(t) = K$, $t \geq -\tau$, is a solution of Eq. (4) since

$$\dot{K} = 0 = K(r - mK).$$

K is a steady state solution of Eq. (4). The other steady state solution of Eq. (4) is $N = 0$ (zero solution). Eq. (7) has only one steady state solution, namely the zero solution. Since

$$f(x) = r(1 - e^x) = -rx + r(1 - e^x + x) = -rx + rx\frac{1 + x - e^x}{x},$$

where

$$\frac{1 + x - e^x}{x} \to 0, \text{ as } x \to 0,$$

the linearized version of Eq. (7) is as follows:

$$\dot{y}(t) = -ry(t - \tau), \qquad t \geq 0. \tag{9}$$

As for ODEs, we seek a solution of the form $y(t) = e^{\lambda t}$ where λ is a real or complex parameter. In that case

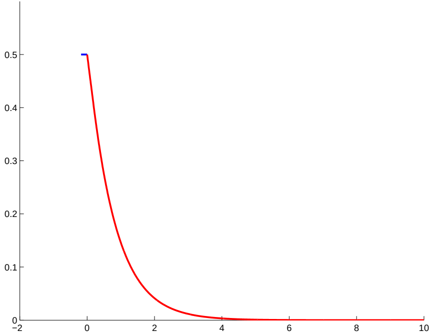
$$\dot{y}(t) = \lambda e^{\lambda t} = -re^{\lambda(t-\tau)} = -re^{-\lambda\tau}e^{\lambda t}, \qquad t \in \mathbb{R}.$$

This results in the so called characteristic equation for λ:

$$\lambda = -re^{-\lambda\tau}, \tag{10}$$

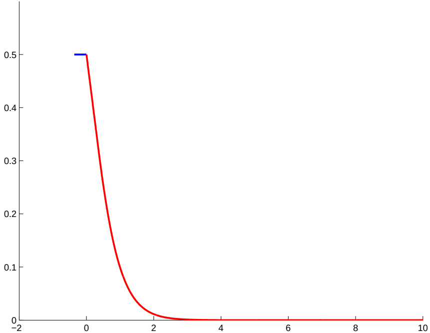
or equivalently

$$\lambda\tau = -r\tau e^{-\lambda\tau}.$$



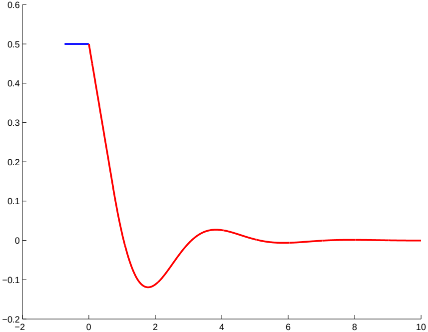
$r\tau = 1/2e$

asymptotically stable, non-oscillatory



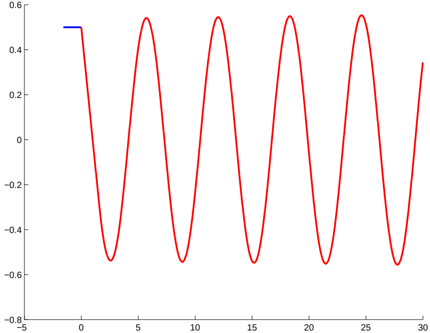
$r\tau = 1/e$

asymptotically stable, non-oscillatory



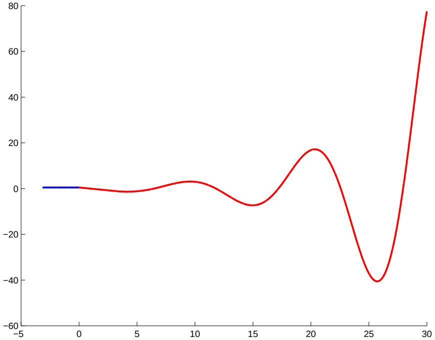
$$r\tau = 2/e$$

asymptotically stable, oscillatory



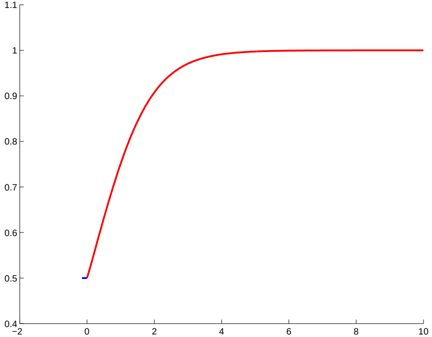
$$r\tau = \pi/2$$

stable, oscillatory, there is periodic solution

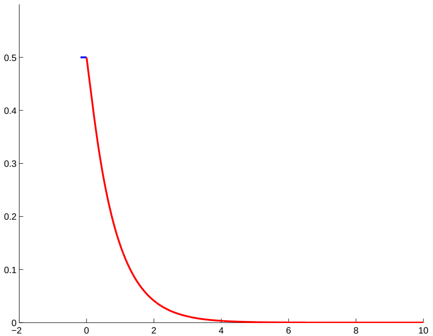


$$r\tau = \pi$$

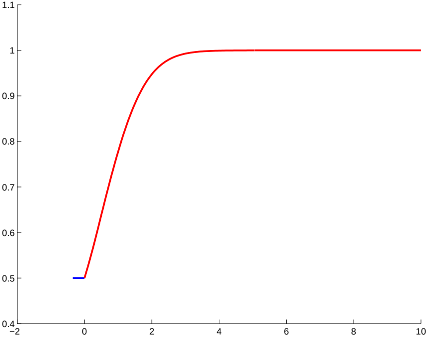
unstable, oscillatory, most of the solutions are unbounded



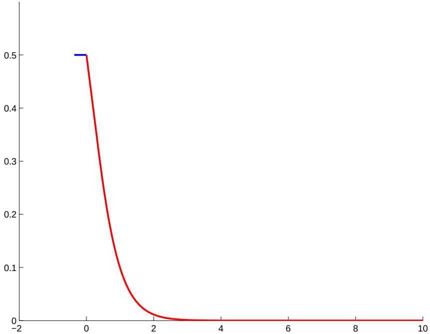
nonlinear ($\tau = 1/2e$)



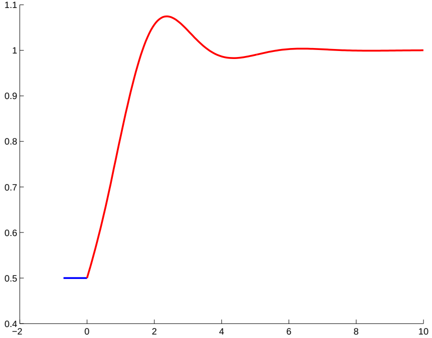
linear ($r\tau = 1/2e$)



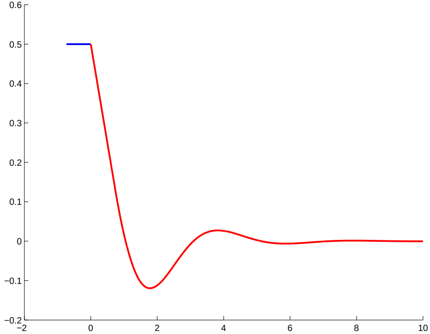
nonlinear $(r\tau = 1/e)$



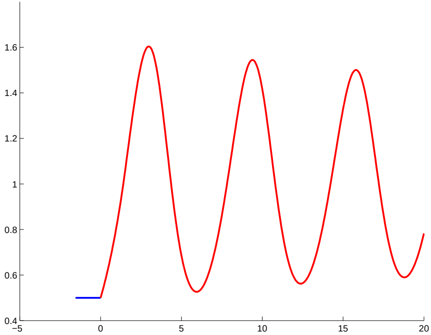
linear $(r\tau = 1/e)$



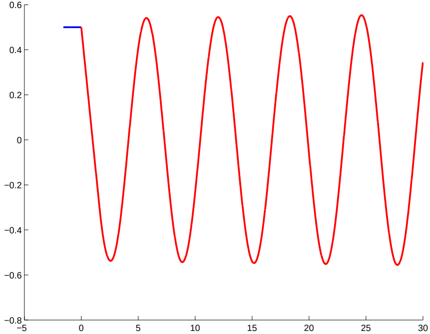
nonlinear ($\tau = 1/2e$)



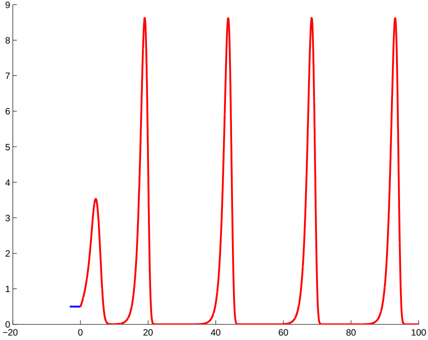
linear ($r\tau = 1/2e$)



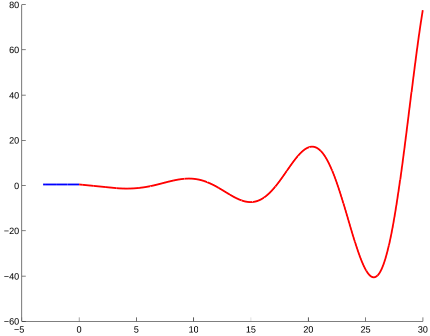
nonlinear ($r\tau = \pi/2$)



linear ($r\tau = \pi/2$)



nonlinear ($\tau = \pi$)



linear ($r\tau = \pi$)

$$\dot{y}(t) = -ry(t-\tau) \tag{9}$$

$$\lambda = -re^{-\lambda\tau} \tag{10}$$

From the general theory of the linear delay differential equations we get the following stability type results.

Theorem 1.

Let $r > 0$ *and* $\tau \geq 0$ *be fixed. The following statements are equivalent:*

(i) *For any solution* $y : [-\tau, \infty) \to \mathbb{R}$ *of (9),* $y(t) \to 0,\ t \to +\infty$.

(ii) *For any solution* $\lambda \in \mathbb{C}$ *of (10),* $\operatorname{Re}\lambda < 0$.

(iii) $r\tau < \frac{\pi}{2}$.

$$\dot{y}(t) = -ry(t-\tau) \tag{9}$$

$$\lambda = -re^{-\lambda\tau} \tag{10}$$

Theorem 2.

Let $r > 0$ *and* $\tau \geq 0$ *be fixed. The following statements are equivalent:*

(i) *Any solution* $y : [-\tau, \infty) \to \mathbb{R}$ *of (9), is bounded on* $[0, \infty)$.

(ii) *For any solution* $\lambda \in \mathbb{C}$ *of (10),* $\mathrm{Re}\,\lambda \leq 0$.

(iii) $r\tau \leq \frac{\pi}{2}$.

$$\lambda = -re^{-\lambda\tau} \tag{10}$$

If $r\tau = \frac{\pi}{2}$, then $\lambda = \frac{\pi}{2\tau} i$ is a solution of the characteristic equation (10), and so the complex valued function

$$y(t) = e^{\frac{\pi}{2\tau} it} = \cos \frac{\pi}{2\tau} t + i \sin \frac{\pi}{2\tau} t$$

is a solution of Eq. (9).
This yields the next corollary.

Corollary 3.

If $r\tau = \frac{\pi}{2}$ then all solutions of Eq. (10) are bounded on $\mathbb{R}_+$, moreover the periodic functions

$$y_1(t) = \cos \frac{\pi}{2\tau} t \qquad \text{and} \qquad y_2(t) = \sin \frac{\pi}{2\tau} t, \qquad t \geq 0,$$

are solutions of Eq. (9) on $\mathbb{R}_+$.

$$\dot{y}(t) = -ry(t-\tau) \tag{9}$$

$$\lambda = -re^{-\lambda\tau} \tag{10}$$

The next result is complementary to Theorems 1 and 2.

Theorem 4.

Let $r > 0$ and $\tau \geq 0$ be fixed. The following statements are equivalent:

(i) *Eq. (9) has an unbounded solutin on* $\mathbb{R}_+$.

(ii) *Eq. (10) has a root* $\lambda \in \mathbb{C}$ *with* $\operatorname{Re}\lambda > 0$.

(iii) $r\tau > \frac{\pi}{2}$.

Oscillation results

Definition 5.

We say that a function $y:\mathbb{R}_+\to\mathbb{R}$ is oscillatory on $\mathbb{R}_+$ if there exist two sequences $(t_n')_{n\geq 1}$ and $(t_n'')_{n\geq 1}$ such that $t_n', t_n''\to\infty$, $\to+\infty$, and $y\left(t_n'\right)<0<y\left(t_n''\right)$, $n\geq 1$.

It is clear that $y:\mathbb{R}_+\to\mathbb{R}$ is not oscillatory on $\mathbb{R}_+$ if and only if there is a $T>0$, such that $|y(t)|>0$, $t\geq T$, or equivalently either y is eventualy positive or eventualy negative.

$$\dot{y}(t) = -ry(t-\tau) \tag{9}$$

$$\lambda = -re^{-\lambda\tau} \tag{10}$$

Theorem 6.

Let $r > 0$ and $\tau \geq 0$ be fixed. The following statements are equivalent.

(i) *Every solution of Eq.(9) is oscillatory on $\mathbb{R}_+$.*

(ii) *The characteristic equation (10) does not have real root.*

(iii) $r\tau > \frac{1}{e}$.

We say for the linear equation (9):

It is stable if any solution of it is bounded on $\mathbb{R}_+$.

It is asymptotically stable if any solution of it tends to zero as $t \to +\infty$.

It is oscillatory if any solution of it oscillates on $\mathbb{R}_+$.

$$\dot{y}(t) = -ry(t-\tau) \tag{9}$$

Summary of the qualitative properties of the solutions of (9):

$0 \le r\tau \le \frac{1}{e}$	not oscillatory	aymptotically stable
$1/e < r\tau < \frac{\pi}{2}$	oscillatory	aymptotically stable
$r\tau = \frac{\pi}{2}$	oscillatory	stable, has periodic solutions
$r\tau > \frac{\pi}{2}$	oscillatory	not stable, has unbounded solution

Let $N(t)$ be the size of the population at time t, and let A be the maximal possible age in the population. From theoretical point of view we assume that $0 < A \leq \infty$, and let $I = [0, A]$ if $A < \infty$ and $I = [0, \infty)$ if $A = \infty$.

Let $u(t, \cdot) : I \to \mathbb{R}_+$ be the density of the distribution of individuals in the popultion of age a at time t.

In that case the size of the population at time t is given by

$$N(t) = \int_0^A u(t, a)\, da.$$

Let $h > 0$ be the time increase, and consider the difference

$$u(t + h, a + h) - u(t, a).$$

Assuming that this difference is approximatly linear in h we have

$$u(t + h, a + h) - u(t, a) = \beta(t, a)u(t, a)h + o(h)h$$

where $\beta : \mathbb{R}_+ \times I \to \mathbb{R}_+$ is a given rate function and $o(h) \to 0, \quad h \to 0$.
Thus the directional derivative

$$D_{t,a}u(t,a) := \lim_{h \to 0+} \frac{u(t+h, a+h) - u(t,a)}{h}$$

exists and

$$D_{t,a}u(t,a) = \beta(t,a)u(t,a), \qquad (t,a) \in \mathbb{R}_+ \times I. \tag{11}$$

The model equation (11) is not sufficient to determine the density function in a unique way. We need to know the initial population distribution $u_0 : I \to \mathbb{R}_+$ and the number of newborns (births) in the population $u(t,0)$.
Thus the complete model is the following:

$$\left.\begin{array}{rcll} D_{t,a}u(t,a) & = & \beta(t,a)u(t,a), & t \geq 0, \quad 0 \leq a < A, \\ u(t,0) & = & g(t, u((t,\cdot)), & t \geq 0, \\ u(0,a) & = & u_0(a), & 0 \leq a < A, \end{array}\right\} \tag{12}$$

where $g(t,\cdot) : \mathbb{R}_+ \times C(I, R_+) \to \mathbb{R}_+$ and $u_0 : I \to \mathbb{R}_+$.

If u is partially differentiable in both variables t and a, then

$$D_{t,a}u(t,a) = \frac{\partial}{\partial t}u(t,a) + \frac{\partial}{\partial a}u(t,a)$$

and hence problem (12) is equivalent to

$$\left.\begin{array}{rcll} \frac{\partial}{\partial t}u(t,a) + \frac{\partial}{\partial a}u(t,a) & = & \beta(t,a)u(t,a), & t \geq 0, \quad 0 \leq a < A, \\ u(t,0) & = & g(t,u((t,\cdot)), & t \geq 0, \\ u(0,a) & = & u_0(a), & 0 \leq a < A. \end{array}\right\} \tag{13}$$

Problem (13) is called the *McKendrick/Von Foerster model.*
Let

$$\gamma(t,a) = \begin{cases} \int\limits_0^t \beta(s, a-t+s)ds, & 0 \leq t < a < A, \\ \int\limits_0^a \beta(t-a+s, s)ds, & 0 \leq a \leq t. \end{cases}$$

Then

$$D_{t,a}\gamma(t,a) = \beta(t,a), \qquad t \geq 0, \quad 0 \leq a < A,$$

and

$$D_{t,a}\left(u(t,a)e^{-\gamma(t,a)}\right) = \left(D_{t,a}u(t,a)\right)e^{-\gamma(t,a)} - u(t,a)\left(D_{t,a}\gamma(t,a)\right)e^{-\gamma(t,a)},$$

and hence

$$D_{t,a}\left(u(t,a)e^{-\gamma(t,a)}\right) = 0, \qquad t \geq 0, \quad 0 \leqslant a < A. \tag{14}$$

But for any continuous function $x : [-A, \infty) \to \mathbb{R}_+$, the function

$$v(t,a) = x(t-a), \qquad t \geq 0, \quad 0 \leq a < A,$$

satisfies

$$\begin{aligned} D_{t,a}v(t,a) &= \lim_{h\to 0}\frac{v(t+h,a+h)-v(t,a)}{h} \\ &= \lim_{h\to 0}\frac{x(t+h-(a+h))-x(t-a)}{h} = 0. \end{aligned}$$

Therefore the function

$$u(t,a) = e^{\gamma(t,a)}x(t-a), \qquad t \geq 0, \quad 0 \leq a < A, \tag{15}$$

satisfies (14) and equivalently (11) on $\mathbb{R}_+ \times [0, A)$. Here x is an arbitrary continuous function. But $u(t,a)$ defined in (15) is a solution of problem (12) if and only if

$$u(t,0) = e^{\gamma(t,0)}x(t) = g(t, e^{\gamma(t,\cdot)}x(t-\cdot))$$

and

$$u(0,a) = e^{\gamma(0,a)}x(-a) = u_0(a), \qquad 0 \leq a < A.$$

So the function $u(t,a)$ defined by (15) is a solution of problem (12) whenever the continuous function $x : [-A, \infty) \longrightarrow \mathbb{R}_+$ satisfies

$$x(t) = e^{-\gamma(t,0)} g\left(t, e^{\gamma(t,\cdot)}x(t-\cdot)\right), \qquad t \geq 0, \tag{16}$$

and

$$x(s) = e^{-\gamma(0,-s)}u_0(-s), \qquad -A < s \leq 0. \tag{17}$$

Special cases:

(I) The number of the newborns are given by using a so-called fertility function $\lambda : \mathbb{R}_+ \times [0, A) \longrightarrow \mathbb{R}_+$. Namely

$$g(t, u(t, \cdot)) = \int_0^A \lambda(t, a) u(t, a) da, \qquad t \in \mathbb{R}_+.$$

By using (16) and (17) this gives

$$x(t) = \begin{cases} \int_0^A \lambda(t, a) e^{\gamma(t,a)} x(t-a)\, da, & t \geq 0, \\ e^{-\gamma(0,-t)} u_0(-t), & -A < t \leq 0. \end{cases} \tag{18}$$

(I/1) $A = +\infty$. Then (18) reduces to

$$x(t) = \int_0^t \lambda(t,a) e^{\gamma(t,a)} x(t-a)\, da + h(t), \qquad t \geq 0, \tag{19}$$

where

$$h(t) = \int_t^\infty \lambda(t,a) e^{\gamma(t,a)} u_0(a-t)\, da, \qquad t \geq 0.$$

Eq. (19) is the so called Volterra-type integral equation. If for any $(t,a) \in \mathbb{R}_+ \times [0,A)$, $\beta(t,a) = 0$ and $\lambda(t,a) = \lambda_0(a)$, then $\gamma(t,a) = 0$, $(t,a) \in \mathbb{R}_+ \times [0,A)$, moreover Eq. (19) can be written in the form

$$x(t) = \int_0^t \lambda_0(a) x(t-a)\, da + h(t), \qquad t \geq 0.$$

This latter equation is the well-known Volterra-type renewal integral equation.

(I/2) $\quad 0 < A < \infty, \;\; \beta(t,a) = 0$ and $\lambda(t,a) = \lambda_0$ (const.), $(t,a) \in \mathbb{R}_+ \times [0,A)$. In that case $\gamma(t,a) = 0, (t,a) \in \mathbb{R}_+ \times [0,A)$ and

$$\int_0^A \lambda(t,a) e^{\gamma(t,a)} x(t-a)\, da = \lambda_0 \int_0^A x(t-a)\, da = \lambda_0 \int_{t-A}^{t} x(s)\, ds, \qquad t \geq 0.$$

Thus (18) can be written in the form

$$x(t) = \begin{cases} \lambda_0 \int_{t-A}^{t} x(s)\, ds, & t \geq 0, \\ u_0(-t), & -A \leq t \leq 0. \end{cases}$$

By differentiation we get

$$\begin{aligned} \dot{x}(t) &= \lambda_0 x(t) - \lambda_0 x(t-A), \qquad t \geq 0, \\ x(t) &= u_0(-t) \qquad -A \leq t \leq 0. \end{aligned}$$

This means that the solution of the age dependent model is equivalent to the solution of the above delay differential equation.

Such type of models were derived by Blythe at. al (1982) from the above age structured model and also by Cooke and Yorke (1973) based on different ideas.

(II) Let us assume that there exists a definite maturation time $\tau \in (0, \infty)$ in the cell population at which the cells multiply by bipartition. Such a case was modelled by M.E. Gurtin in his paper "Some questions and open problems in continuum mechanics and population dynamics J. Diff. Eqns. 48 (1983), 353–359".

The birth rate function is defined by

$$g(t, u(t, \cdot)) = g_0(t, u(t, \tau))$$

where $g_0 : \mathbb{R}_+^2 \longrightarrow \mathbb{R}_+$ is continuous.

In that case (16) and (17) reduce to the delay functional equation

$$x(t) = \begin{cases} g_0\left(t, e^{\gamma(t,\tau)} x(t-\tau)\right) & 0 < t, \\ u_0(-t), & -A \leqslant t \leq 0. \end{cases}$$

The Lotka-Volterra equations (frequently named as predator-prey equations) were proposed independently by Alfred J. Lotka in 1925 and Vito Volterra in 1926. The equations

$$\dot{x}_1 = x_1(\gamma_1 - a x_2)$$

$$\dot{x}_2 = -x_2(\gamma_2 - b x_1)$$

where

$x_1 = x_1(t)$ is the number of some prey (e.g., rabbits) at time t;
$x_2 = x_2(t)$ Is the number of some predator (e.g., foxes) at time t;
γ_1, γ_2, a, b are positive parameters representing the interaction of the two species.
Physical meaning of the prey equation:

$$\dot{x}_1 = \gamma_1 x_1 - a x_1 x_2.$$

Prey have unlimited food supply and it is assumed that the size of the prey population is growing exponentially unless subject to predation. This exponential growth is represented by the term $\gamma_1 x_1$.

The term ax_1x_2 represents the rate of predation upon the prey is proportional to the rate at which the predators and the prey meet.
Physical meaning of the predator equation:

$$\dot{x}_2 = -\gamma_2 x_2 + b x_2 x_1.$$

Here bx_2x_1 is the growth rate of the predator population and $\gamma_2 x_2$ represents the natural death of the predators.
Equilibrium occurs in the model when neither of the population sizes is changing, i.e. when the right hand sides of the differential equations are equal to 0:

$$x_1 (\gamma_1 - a x_2) = 0$$

$$-x_2 (\gamma_2 - b x_1) = 0.$$

This holds if either $x_1 = x_2 = 0$ or $x_1 = \frac{\gamma_2}{b},\ x_2 = \frac{\gamma_1}{a}$.
Hence there are two equilibria.

The general case for n-species:

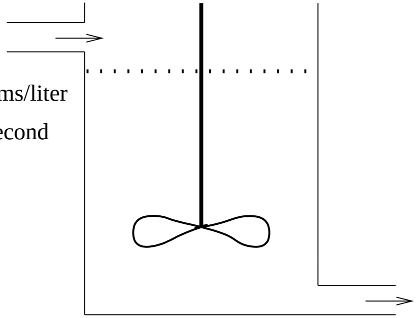
$$\begin{aligned} \dot{x}_i &= x_i\left(\gamma_i + \sum_{j=1}^{n} a_{ij}x_j\right), \qquad 1 \leq i \leq n \\ x_i(0) &= x_{i0}, \qquad 1 \leq i \leq n. \end{aligned}$$

The most usually used version of the delayed Lotka-Volterra differential equations for n-species

$$\begin{aligned} \dot{x}_i(t) &= x_i(t)\left(\gamma_i + \sum_{j=1}^{n}\left(\alpha_{ij}x_j(t) + \beta_{ij}x_j(t-\tau_{ij}) + \int_0^t \gamma_{ij}(t-s)x_j(s)\,ds\right)\right) \\ x_i(t) &= \varphi_i(t), \qquad -\tau \leq t \leq 0, \end{aligned}$$

for any $1 \leqslant i \leqslant n$, where $\gamma_i, \alpha_{ij}, \beta_{ij} \in \mathbb{R}$, $\tau_{ij} \in \mathbb{R}_+$, $\gamma_{ij} \in C(\mathbb{R}_+, \mathbb{R})$, $1 \leqslant i, j \leqslant n$, and $\varphi_i \in C([-\tau, 0], \mathbb{R}_+)$, where $\tau = \max_{1 \leqslant i,j \leqslant n} \tau_{ij}$.

First we shall study the problem of adjusting the concentration of salt to a desired level in a brine mixing tank.



A $t = 0$ the tank contains V liters of brine with an initial salt concentraton of c_0 grams per liter. The salt concentration in the incoming brine is s gram per liter.

Our task is to adjust s, the incoming concentration of salt, so that the concentration of salt in the thank attains (and remains at) a predetermined concentration k.

Our basic relation is

$$\frac{d}{dt}(cV) = (\text{Rate in}) - (\text{Rate out}),$$

where $c = c(t)$ denotes the homogeneous concentration in the tank at time t.
But

$$\text{Rate in} = s \text{ (grams/liter)} \times r \text{ (liters/second)}$$

$$\text{Rate out} = c \text{ (grams/liter)} \times r \text{ (liters/second)}.$$

So the governing equation is

$$\frac{d}{dt}(cV) = sr - cr,$$

and hence

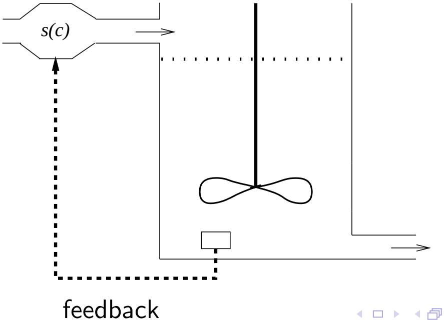
$$\frac{dc}{dt} = ps - pc, \qquad p = \frac{r}{V} \text{ (constant)}, \tag{20}$$

with initial condition $c(0) = c_0$.

The solution is

$$c(t) = s + (c_0 - s)\, e^{-pt} \qquad t \geq 0.$$

From the above formula it is clear that our task cannot be accomplished in finite time, and it can be done at infinity if and only if $s = k$.
To overcome this difficulty, we must introduce the notion of a feedback control law wich governs s.



The concentration c of salt in the tank is measured at any instant, and the inflow rate is controled by the instant value of c.
With this control law, the differential equation (20) now becomes

$$\frac{dc}{dt} = ps(c) - pc, \tag{21}$$

and the form of the solution depends on the initial concentration $c(0) = c_0$.
A simple example of a feedback control law is the following one:

$$s = s(c) = \begin{cases} 0 & \text{if } c > k, \\ k & \text{if } c = k, \\ z & \text{if } c < k, \end{cases}$$

where z is some convenient value greater than k.
The possible solutions depending on c_0.
Case 1: If $c_0 > k$, then $s(c) = 0$ and the solution of Eq. (21) is

$$c(t) = c_0 e^{-pt}, \qquad t \geq 0.$$

The desired concentration will be attained at $t = t^*$, where $c(t^*) = k$.
Hence $t^* = \frac{1}{p} \ln\left(\frac{c_0}{k}\right)$.
Case 2: If $c_0 = k$, then $s(c) = k$, $c(t) = k$, and $t^* = 0$.
Case 3: If $c_0 < k$, then $s(c) = z$ and from Eq. (21) the solution is

$$c(t) = z + (c_0 - z)\, e^{-pt},$$

where $z > k > c_0$. The desired concentration will be obtained when $c(t^*) = k$, and this gives

$$t^* = \frac{1}{p} \ln\left(\frac{z - c_0}{z - k}\right).$$

So the problem is solved from theoretical point of view. In the practice the following modified versions are more realistic.
(1) The inflow rate a time t depends on the result of the measurement at an earlier time $t - \tau$, where τ is a positive time delay.
So the governing equation is a delay differential equation

$$\dot{c}(t) = ps(c(t - \tau)) - pc(t), \qquad t \geq 0, \qquad (22)$$

with the initial condition

$$c(t) = c_0, \qquad -\tau \le t \le 0.$$

(ii) In the above models the measurement is continuous which can be technicaly complicated and also expensive.
Assume we take samples at the following discrete moments

$$0, \quad h, \quad 2h, \quad \dots, \quad nh, \quad \dots$$

where $h > 0$ is the sampling time. The control function is

$$u(t) = ps\left(c\left(\left[\frac{t}{h}\right]h - kh\right)\right), \qquad t \ge 0,$$

where k is a fixed positive integer and $[\cdot]$ denotes the greatest integer part function.
So the governing equation is

$$\dot{c}(t) = ps\left(c\left(\left[\frac{t}{h}\right]h - kh\right)\right) - pc(t), \qquad t \ge 0, \tag{23}$$

with the initial condition

$$c(t) = c_0, \qquad -kh \le t \le 0.$$

Eq. (23) is called equation with piecewise constant argument (EPCA). Eq. (23) is also called "hybrid" delay differential equation. Its solution leads to the solution of some related discrete difference equation. Namely,

$$c(t) = e^{-p(t-nh)}c(nh)+e^{-pt}\int_{nh}^{t} e^{pu}ps\left(c\left(\left[\frac{u}{h}\right]h-kh\right)\right)du, \qquad nh \le t < (r$$

But $n \le \frac{u}{h} \le \frac{t}{h} < n+1$, and hence

$$c(t) = e^{-p(t-nh)}c(nh)+e^{-pt}(e^{pt}-e^{pnh})s(c((n-k)h)), \qquad nh \le t < (n+1)h.$$

Thus we arrive to the difference equation

$$c((n+1)h) = e^{-ph}c(nh) + (1-e^{-ph})s(c((n-k)h)), \qquad n \ge 0.$$

The solution of Eq. (23) is given by

$$c(t) = \frac{c((n+1)h) - c(nh)}{h}(t-nh) + c(nh), \qquad 0 \le nh \le t < (n+1)h.$$