

JOANNA SKONIECZNA and URSZULA FORYŚ (Warszawa)

STABILITY SWITCHES FOR SOME CLASS OF DELAYED POPULATION MODELS

Abstract. We study stability switches for some class of delay differential equations with one discrete delay. We describe and use a simple method of checking the change of stability which originally comes from the paper of Cook and Driessche (1986). We explain this method on the examples of three types of prey-predator models with delay and compare the dynamics of these models under increasing delay.

1. Introduction. Typically, population models are described using ordinary differential equations (see e.g. [10, 5] and the review in [1]). However, it is sometimes biologically relevant to consider time delays present in many processes in nature. Therefore, instead of ODEs we study delay differential equations describing the dynamics of populations and interactions between them.

In this paper we describe and explain, on the basis of some population models, a method of studying stability switches for systems of delay differential equations with one discrete delay. The idea of this method comes from [2]. However, it is still not well recognised in the literature. It turns out that in many cases to study the change of stability of the steady state it is enough to check the derivative of some auxiliary function at the critical point $z_0 = \omega_0^2$, where $\pm i\omega_0$ is a pair of purely imaginary eigenvalues for a critical value of delay τ_0 . On the other hand, although different types of prey-predator models with time delays have been studied in many papers and text -books, it is not easy to find a comparison between the dynamics of systems that have origins in different ecological assumptions. Therefore,

2010 *Mathematics Subject Classification*: Primary 34K13, 34K28, 34K60, 37N25.

Key words and phrases: delay differential equations, stability, stability switches, Hopf bifurcation, prey-predator model, trophic level.

we apply our method to three types of prey-predator models with delay and compare the influence of delays on the dynamics of these systems.

Typically, studying the stability of some steady state one uses the method of linearisation (see e.g. [6]). For the resulting linear system we find the characteristic equation, also called the transcendental equation (for a similar type of transcendental equation see e.g. [7]). The characteristic function is usually not a polynomial, but a combination of some polynomials and the exponential function. It is well known that time delay can have destabilising influence, as in the case in the most exploited delayed population model given by the Hutchinson equation [8]. Therefore, it is of great importance to study the stability of the steady state which is stable for the system without delay under the influence of increasing delay. In such a case the real parts of the characteristic values are negative in the absence of delay. As long as these real parts are negative, the steady state is stable. Note that the characteristic values are roots of analytic functions, and hence depend on the model parameters, and this dependence is as smooth as the right-hand side of the system under study (see [6]). We focus on the dependence of the stability on the time delay. The stability may change and a bifurcation can occur at a threshold value of the delay for which there exist a pair of purely imaginary eigenvalues. A change of stability appears at such a threshold if the characteristic values cross the imaginary axis from left to right and then the steady state loses stability. On the other hand, if the steady state is unstable for delays smaller than the threshold, then it can gain stability. Namely, if we know that there is only one pair of eigenvalues with positive real part and the characteristic values pass from the right to the left half-plane, then this point can gain stability. This direction is described by the sign of the real part of the derivative of the characteristic values with respect to the bifurcation parameter. If this parameter is positive, the steady state becomes unstable. If it is negative, it can become stable.

The paper is organised as follows. In Section 2 we present the main theorem which is applied in Section 3 to study stability switches for three types of prey-predator models. Section 4 is devoted to the discussion of results and presents some hints towards general applications of the method described.

2. Main Theorem. In this article we focus on systems of delay differential equations with one discrete delay (see [2]). We are interested in DDEs for which the characteristic function has a special form

$$(2.1) \quad W(\lambda) = P(\lambda) + Q(\lambda)e^{-\tau\lambda} = \sum_{k=0}^{n_0} a_k \lambda^k + \sum_{k=0}^{n_1} b_k \lambda^k e^{-\tau\lambda}, \quad n_0 > n_1,$$

where a_k are real numbers and Q has no roots on the imaginary axis.

In this section we present the main theorem concerning stability changes. We assume that for the steady state we study, the characteristic function has the form (2.1), and this state is stable for $\tau = 0$. Then the real parts of all eigenvalues are negative. We would like to check whether the steady state can become unstable for some positive values of τ . As each eigenvalue is a continuous function of τ , a necessary condition for a stability change is the existence of some critical value τ_0 of delay for which there are eigenvalues on the imaginary axis.

Therefore, the characteristic function (2.1) must have a purely imaginary root. We shall find that point. As there exist two roots with positive and negative imaginary part, we focus on finding the positive one.

DEFINITION 2.1. Let us define two auxiliary functions $f, g : \mathbb{R}^+ \rightarrow \mathbb{R}$:

$$(2.2) \quad g(y) = |P(iy)|^2 - |Q(iy)|^2 \quad \text{and} \quad f(y) = g(\sqrt{y}).$$

Note that at a point where the stability is lost the function g is equal to zero. Therefore, we are interested in finding points where $g(y) = 0$. Next, we calculate the values τ_k of delay such that $W(iy) = 0$. The form of (2.1) implies that for any purely imaginary eigenvalue $\lambda = iy$ there may exist a sequence of critical values of delays. Finally we check the sign of the derivative $\left. \frac{d\Re\lambda(\tau)}{d\tau} \right|_{\tau=\tau_k}$. If this sign is positive, the steady state loses stability, while if it is negative, the stationary point remains stable.

MAIN THEOREM 2.2. *If the characteristic function has the form (2.1) and Q has no roots on the imaginary axis, then the derivative $\left. \frac{d\Re\lambda(\tau)}{d\tau} \right|_{\tau=\tau_k}$, where $\tau_k, k \in \mathbb{N}$, denote the threshold values of delay, has the same sign as $f'(y^2)$, where the auxiliary function f is defined in (2.2), and $\lambda(\tau_k) = iy$.*

Proof. Assume that for the threshold values τ_k the characteristic function $W(\lambda)$ has an imaginary root $\lambda = iy$. We would like to find the sign of $\left. \frac{d\Re\lambda(\tau)}{d\tau} \right|_{\tau=\tau_k}$ for $\tau = \tau_k$. Let $\lambda = x + iy$. We differentiate (2.1) with respect to τ for $\tau = \tau_k$, that is, at $x = 0$. We have

$$\begin{aligned} 0 &= W'(x + iy)|_{x=0} \\ &= P'(iy)(x' + iy') - Q(iy)e^{-iy\tau}((x' + iy')\tau + iy) + Q'(iy)e^{-iy\tau}(x' + iy'). \end{aligned}$$

For $\lambda = iy$, we have $x = 0$ and $P(iy) = -Q(iy)e^{-iy\tau}$, $P(iy)/Q(iy) = -e^{-iy\tau}$. Hence,

$$W'(iy) = P'(iy)(x' + iy') + P(iy)((x' + iy')\tau + iy) - Q'(iy)\frac{P(iy)}{Q(iy)}(x' + iy').$$

We define

$$(2.3) \quad \begin{aligned} P_{1r}(y) &:= \Re P(iy), & P_{1i} &:= \Im P(iy), \\ P_{2r}(y) &:= \Re P'(iy), & P_{2i} &:= \Im P'(iy), \\ Q_{1r}(y) &:= \Re Q(iy), & Q_{1i} &:= \Im Q(iy), \\ Q_{2r}(y) &:= \Re Q'(iy), & Q_{2i} &:= \Im Q'(iy), \end{aligned}$$

and notice that

$$\begin{aligned} P'_{1r}(y) &= -P_{2i}(y), & P'_{1i}(y) &= P_{2r}(y), \\ Q'_{1r}(y) &= -Q_{2i}(y), & Q'_{1i}(y) &= Q_{2r}(y). \end{aligned}$$

Now we can rewrite $W'(iy)$ using its real and imaginary part and (2.3):

$$\begin{cases} 0 = \Re W'(iy) = ax' - by' - P_{1i}y, \\ 0 = \Im W'(iy) = bx' + ay' + P_{1r}y, \end{cases}$$

where

$$\begin{aligned} a &= P_{2r} + \tau P_{1r} \\ &\quad + \frac{1}{Q_{1r}^2 + Q_{1i}^2} (P_{1i}Q_{1r}Q_{2i} - P_{1r}Q_{1r}Q_{2r} - P_{1i}Q_{1i}Q_{2r} - P_{1r}Q_{1i}Q_{2i}), \\ b &= P_{2i} + \tau P_{1i} \\ &\quad + \frac{1}{Q_{1r}^2 + Q_{1i}^2} (P_{1r}Q_{1i}Q_{2r} - P_{1i}Q_{1i}Q_{2i} - P_{1i}Q_{1r}Q_{2r} - P_{1r}Q_{1r}Q_{2i}). \end{aligned}$$

After solving the equations above we obtain

$$x' = \frac{y(P_{1i}a - P_{1r}b)}{a^2 + b^2}.$$

The sign of x' depends only on $y(P_{1i}a - P_{1r}b)$, where

$$P_{1i}a - P_{1r}b = P_{1i}P_{2r} - P_{1r}P_{2i} - (Q_{1i}Q_{2r} - Q_{1r}Q_{2i}) \frac{P_{1i}^2 + P_{1r}^2}{Q_{1r}^2 + Q_{1i}^2}.$$

Therefore,

$$(2.4) \quad \text{sign}(x') = \text{sign} \left(y \left(P_{1i}P_{2r} - P_{1r}P_{2i} - (Q_{1i}Q_{2r} - Q_{1r}Q_{2i}) \frac{P_{1i}^2 + P_{1r}^2}{Q_{1r}^2 + Q_{1i}^2} \right) \right).$$

Now, we consider $f'(y^2)$, where f and g are defined by (2.2). Note that

$$g(y) = P_{1r}^2(y) + P_{1i}^2(y) - Q_{1r}^2(y) - Q_{1i}^2(y),$$

so

$$g'(y) = 2P_{1r}(y)P'_{1r}(y) + 2P_{1i}(y)P'_{1i}(y) - 2Q_{1r}(y)Q'_{1r}(y) - 2Q_{1i}(y)Q'_{1i}(y),$$

that is,

$$g'(y) = 2P_{1i}(y)P_{2r}(y) - 2P_{1r}(y)P_{2i}(y) - 2Q_{1i}(y)Q_{2r}(y) + 2Q_{1r}(y)Q_{2i}(y).$$

Recalling that $f(y) = g(\sqrt{y})$, we calculate

$$f'(y) = g'(\sqrt{y})(\sqrt{y})' = \frac{P_{1i}(\sqrt{y})P_{2r}(\sqrt{y}) - P_{1r}(\sqrt{y})P_{2i}(\sqrt{y}) - Q_{1i}(\sqrt{y})Q_{2r}(\sqrt{y}) + Q_{1r}(\sqrt{y})Q_{2i}(\sqrt{y})}{\sqrt{y}}$$

and obtain

$$f'(u)|_{u=y^2} = \frac{1}{y}(P_{1i}(y)P_{2r}(y) - P_{1r}(y)P_{2i}(y) - Q_{1i}(y)Q_{2r}(y) + Q_{1r}(y)Q_{2i}(y)).$$

We are looking for \bar{y} such that $W(i\bar{y}) = 0$ and $g(\bar{y}) = 0$. Hence, $P_{1r}^2(\bar{y}) + P_{1i}^2(\bar{y}) = Q_{1r}^2(\bar{y}) + Q_{1i}^2(\bar{y})$, which yields

$$(2.5) \quad \bar{y}f'(u)|_{u=\bar{y}^2} = P_{1i}(\bar{y})P_{2r}(\bar{y}) - P_{1r}(\bar{y})P_{2i}(\bar{y}) - \frac{P_{1r}^2(\bar{y}) + P_{1i}^2(\bar{y})}{Q_{1r}^2(\bar{y}) + Q_{1i}^2(\bar{y})}(Q_{1i}(\bar{y})Q_{2r}(\bar{y}) - Q_{1r}(\bar{y})Q_{2i}(\bar{y})).$$

Comparing (2.5) and (2.4) one gets

$$\begin{aligned} \text{sign}(x') &= \text{sign}\left(y\left(P_{1i}P_{2r} - P_{1r}P_{2i} - (Q_{1i}Q_{2r} - Q_{1r}Q_{2i})\frac{P_{1i}^2 + P_{1r}^2}{Q_{1r}^2 + Q_{1i}^2}\right)\right) \\ &= \text{sign}(y^2 f'(y^2)). \end{aligned}$$

Therefore, $\frac{d\Re\lambda(\tau)}{d\tau}|_{\tau=\tau_k}$, where $\tau_k, k \in \mathbb{N}$, denote the threshold values of delay, has the same sign as $f'(y^2)$. ■

REMARK 2.3. Notice that the assumption that Q has no roots on the imaginary axis can be weakened. One can only require $Q_{1r}^2 + Q_{1i}^2 \neq 0$ in a neighbourhood of the point $i\bar{y}$ which is the eigenvalue for the critical value of delay τ .

3. Stability switches for prey-predator models with delay. Now, we explain the use of the Main Theorem on simple examples coming from population dynamics, namely prey-predator models with delay. In [11] we have also studied the Hutchinson equation using this framework. However, this single equation is simple and very well known and in our opinion it cannot highlight the power of our method. We need an at least two-variable model to describe this method properly.

In this section we present three examples of prey-predator models that have characteristic functions of the form (2.1), and study stability switches using the Main Theorem of the previous section. The original prey-predator model without delay is very well known (see e.g. [10, 5]). We focus on the prey-predator model with carrying capacity for prey because we would like to study the possible destabilisation effect of delay; hence, we require a stable steady state for the system without delay. The relevant system without delay

reads

$$(3.1) \quad \begin{cases} \dot{V}(t) = a_1 V(t) \left(1 - \frac{V(t)}{K}\right) - b_1 V(t) P(t), \\ \dot{P}(t) = -a_2 P(t) + b_2 V(t) P(t), \end{cases}$$

where $V(t)$ and $P(t)$ are the densities of preys and predators, respectively, a_1 is the prey reproduction rate, K is their carrying capacity, b_1 describes the effectiveness of hunting, a_2 is the predator mortality rate and b_2/b_1 reflects the part of hunted biomass which is used for predator reproduction. The term $V(t)P(t)$ is the number of prey-predator encounters and it describes prey-predator interactions.

It is well known that (3.1) always has two steady states

$$(\bar{V}, \bar{P}) \in \{(0, 0), (K, 0)\}$$

and for $K > a_2/b_2$ there exists a third positive steady state

$$(V^*, P^*) = \left(\frac{a_2}{b_2}, \frac{a_1}{b_1} \left(1 - \frac{a_2}{K b_2}\right) \right).$$

The first steady state $(0, 0)$ is always unstable, independently of the model parameters. For $K < a_2/b_2$ the second steady state $(K, 0)$ is stable, while for $K > a_2/b_2$ it is unstable and the positive steady state (V^*, P^*) that exists for such parameter values is stable. Moreover, stable steady states are globally stable in $(\mathbb{R}^+)^2$ (see e.g. [10, 5]).

It is obvious that time delay can be introduced into different terms of (3.1) depending on the model assumptions. In general, we can consider the system with several delays reflecting time lags appearing in different processes in this model. However, two types of prey-predator systems with delay are best known. In the first one, proposed by Wangersky and Cunningham [12], delay is incorporated in prey-predator interactions. On the other hand, May [9] pointed out that from the ecological point of view the three-level trophic system such as the vegetation-herbivore-carnivore system should be more stable than the two-level vegetation-herbivore system. If the two-level trophic system is described by the Hutchinson equation, then adding interactions with predators typically should have a stabilising effect. Therefore, it is of biological relevance to consider the prey-predator model with time delay in the term describing the growth of preys.

Each model is illustrated by a few plots showing dependences between solutions and delay. The plots are made for the same parameters $a_1 = 3$, $a_2 = 1$, $b_1 = 1$, $b_2 = 2$, $k = 3$ and initial data $(V_0, P_0) = (1, 1)$. In each model for small delay the stationary point is stable and loses stability after increasing the delay.

3.1. Prey-predator model with delay: type I. In this subsection we consider two types of models reflecting the idea of delay in the prey-predator interactions term. In this model we assume that the prey reproduction process is very fast, and therefore we do not consider any delay in the equation describing this population. On the other hand, the predator reproduction process is not so fast and we incorporate a time delay in this process. In the first model we consider a time delay in the per capita growth rate, that is, we introduce a delay only in $V(t - \tau)$ leaving the density of predators $P(t)$ at the present time, while in the second model we just add a time delay in the interaction term b_2VP replacing it by $b_2V(t - \tau)P(t - \tau)$.

Now, we assume that the per capita growth rate of predators depends on the number of preys hunt some time ago. Therefore, we consider the following system of delayed differential equations:

$$(3.2) \quad \begin{cases} \dot{V}(t) = a_1V(t)\left(1 - \frac{V(t)}{K}\right) - b_1V(t)P(t), \\ \dot{P}(t) = -a_2P(t) + b_2V(t - \tau)P(t). \end{cases}$$

It is obvious that (3.2) has the same steady states as (3.1). In this paper we focus on the stability of the positive steady state (V^*, P^*) which is stable for $\tau = 0$. We study the change of stability with respect to the delay parameter τ . To check the stability of the steady state we make a linearisation around (V^*, P^*) and after simple calculations we obtain

$$(3.3) \quad \begin{cases} \dot{\tilde{V}}(t) = -\frac{a_1a_2}{Kb_2}\tilde{V}(t) - b_1\frac{a_2}{b_2}\tilde{P}(t), \\ \dot{\tilde{P}}(t) = b_2\frac{a_1}{b_1}\left(1 - \frac{a_2}{Kb_2}\right)\tilde{V}(t - \tau), \end{cases}$$

where \tilde{P} and \tilde{V} are small deviations from P^* and V^* , respectively. The characteristic matrix of (3.3) reads

$$(3.4) \quad \begin{pmatrix} -\frac{a_1a_2}{Kb_2} - \lambda & -b_1\frac{a_2}{b_2} \\ a_1\frac{b_2}{b_1}\left(1 - \frac{a_2}{Kb_2}\right)e^{-\lambda\tau} & -\lambda \end{pmatrix},$$

and the characteristic function which is the determinant of the matrix (3.4) has the form

$$W(\lambda) = \lambda^2 + \frac{a_1a_2}{Kb_2}\lambda + a_1a_2\left(1 - \frac{a_2}{Kb_2}\right)e^{-\lambda\tau} = \lambda^2 + c_1\lambda + c_2e^{-\lambda\tau},$$

which is obviously of the form (2.1). To study stability we check for which values of τ the real parts of the roots of the characteristic function, that is, the eigenvalues of (3.4) are negative. The continuous dependence of eigenvalues on the delay parameter (see e.g. [10, 5]) implies that a change of stability requires the appearance of purely imaginary eigenvalues. Looking for purely

imaginary eigenvalues we follow [2], [3] and formulate the necessary condition $|-y^2 + c_1 iy| = |c_2 e^{-iy\tau}|$, where $\lambda = iy$. As in the Main Theorem, we use the auxiliary functions

$$\begin{aligned} g(y) &= |-y^2 + c_1 iy|^2 - |c_2|^2 = y^4 + c_1^2 y^2 - c_2^2, \\ f(y) &= g(\sqrt{y}) = y^2 + c_1^2 y - c_2^2. \end{aligned}$$

Notice that

$$f'(t)|_{t=y^2} = 2y^2 + c_1^2 > 0.$$

Solving the equation $g(y) = 0$ for $y > 0$ one gets

$$\bar{y}_1 = \sqrt{\frac{\sqrt{c_1^4 + 4c_2^2} - c_1^2}{2}}.$$

To check for which values of τ we have $\lambda = i\bar{y}_1$, we solve

$$\begin{cases} -\bar{y}_1^2 + c_2 \cos(\bar{y}_1 \tau) = 0, \\ c_1 \bar{y}_1 - c_2 \sin(\bar{y}_1 \tau) = 0, \end{cases}$$

and obtain the sequence (τ_k) , $k \in \mathbb{N}$, such that

$$(3.5) \quad \tau_0 = \frac{1}{\bar{y}_1} \arccos\left(\frac{\bar{y}_1^2}{c_2}\right) \quad \text{and} \quad \tau_k = \tau_0 + \frac{2k\pi}{\bar{y}_1}.$$

Finally, the Main Theorem shows that the sign of $\frac{d\Re\lambda(\tau)}{d\tau}|_{\tau=\tau_k}$ is equal to the sign of $f'(\bar{y}^2)$, which is positive for every $k \in \mathbb{N}$. Therefore, the eigenvalues always cross the imaginary axis from left to right, which means that for $\tau = \tau_0$ the steady state (V^*, P^*) loses stability and cannot gain it for larger τ . Indeed, at $\tau = \tau_k$ for $k > 0$ there appears a pair of purely imaginary eigenvalues which again cross the imaginary axis from left to right and the number of eigenvalues with positive real part increases.

Now we consider the second prey-predator model with delay in the prey-predator interaction term:

$$(3.6) \quad \begin{cases} \dot{V}(t) = a_1 V(t) \left(1 - \frac{V(t)}{K}\right) - b_1 V(t) P(t), \\ \dot{P}(t) = -a_2 P(t) + b_2 V(t - \tau) P(t - \tau). \end{cases}$$

As for (3.2), we study stability switches for the steady state (V^*, P^*) , starting from $\tau = 0$ and checking the change of stability for increasing delay.

Firstly, we need to find the characteristic function. After linearisation around (V^*, P^*) one gets

$$\begin{cases} \dot{\tilde{V}}(t) = -\frac{a_1 a_2}{K b_2} \tilde{V}(t) - b_1 \frac{a_2}{b_2} \tilde{P}(t), \\ \dot{\tilde{P}}(t) = \frac{a_1 b_2}{b_1} \left(1 - \frac{a_2}{K b_2}\right) \tilde{V}(t - \tau) - a_2 \tilde{P}(t) + a_2 \tilde{P}(t - \tau). \end{cases}$$

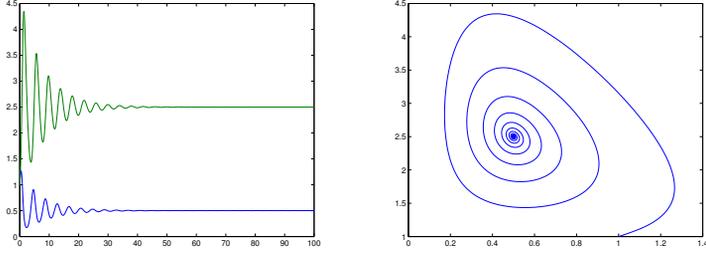


Fig. 1. Plot of solution to (3.2) for $\tau = 0.1$

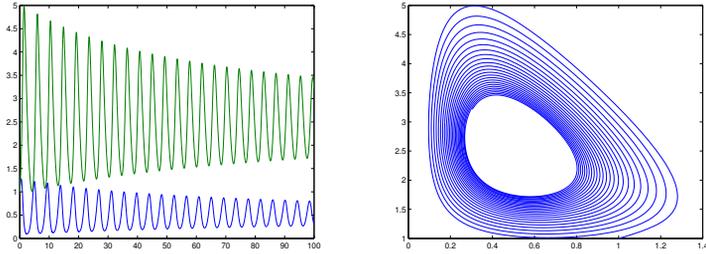


Fig. 2. Plot of solution to (3.2) for $\tau = 0.2$

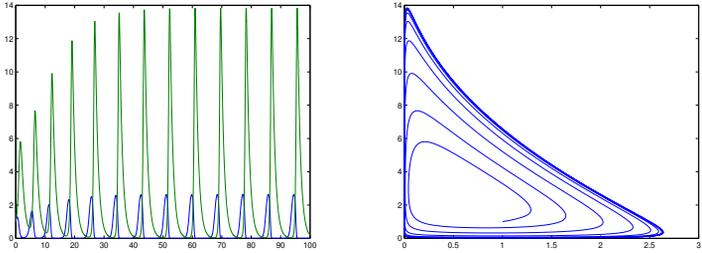


Fig. 3. Plot of solution to (3.2) for $\tau = 0.3$

The characteristic function is

$$W(\lambda) = \lambda^2 + \left(a_2 + \frac{a_1 a_2}{K b_2} \right) \lambda + \frac{a_1 a_2^2}{K b_2} + \left(-a_2 \lambda - 2 \frac{a_1 a_2^2}{K b_2} + a_1 a_2 \right) e^{-\lambda \tau}.$$

We are looking for purely imaginary eigenvalues so that the stability may change. We calculate

$$W(i\omega) = -\omega^2 + (a_2 + c)i\omega + a_2 c + (-a_2 i\omega - 2a_2 c + a_1 a_2) e^{-i\omega \tau},$$

where $c = c_1 = \frac{a_1 a_2}{K b_2}$ and $c < a_1$. We find the auxiliary function

$$g(y) = (-y^2 + a_2 c)^2 + (a_2 + c)^2 y^2 - (a_1 a_2 - 2a_2 c)^2 - a_2^2 y^2,$$

that is,

$$g(y) = y^4 + c^2 y^2 + a_2^2 (4a_1 c - a_1^2 - 3c^2),$$

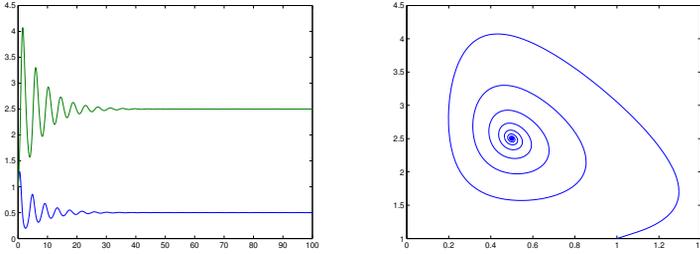


Fig. 4. Plot of solution to (3.6) for $\tau = 0.1$

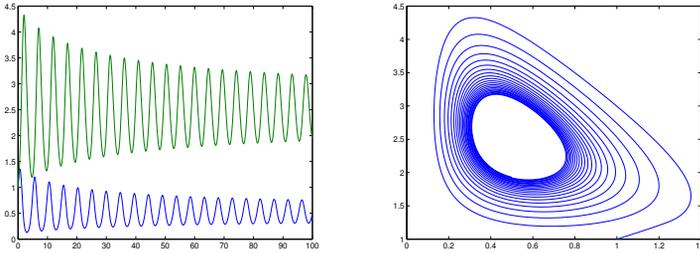


Fig. 5. Plot of solution to (3.6) for $\tau = 0.3$

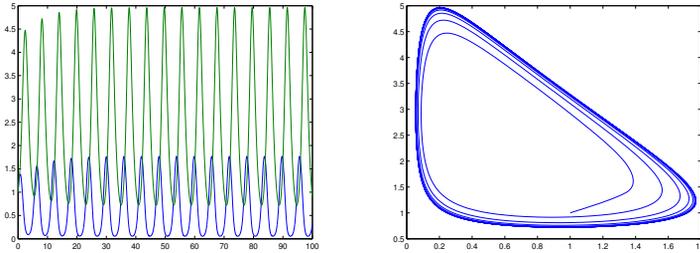


Fig. 6. Plot of solution to (3.6) for $\tau = 0.5$

and the functions f and f' :

$$f(y) = y^2 + c^2y + a_2^2(4a_1c - a_1^2 - 3c^2), \quad f'(y) = 2y + c^2.$$

Note that $f'(y^2) = 2y^2 + c^2$ is always positive.

Now it is necessary to find points such that $g(y) = y^4 + c^2y^2 + a_2^2(4a_1c - a_1^2 - 3c^2) = 0$. This equality can hold if $4a_1c - a_1^2 - 3c^2 < 0$. Therefore, $a_1 < c$ or $a_1 > 3c$. Note that $a_1 < c$ contradicts the existence of a positive steady state (V^*, P^*) we study.

Summing up, the steady state (V^*, P^*) for $3a_2/b_2 > K$ is always stable and the stability switches are not possible. For $3a_2/b_2 < K$ we use the Main Theorem, and the inequality $f'(y^2) > 0$ implies that (V^*, P^*) loses stability for the first critical value τ_0 of delay such that $W(i\bar{y}) = 0$ and cannot gain it for larger τ , as in the case of (3.2).

3.2. Prey-predator model with delay: type II. The next possibility of introducing delay was explained by May [9] and is connected with the ecology rule of increasing stability of trophic systems with increasing number of species involved. Let V be the herbivore density in the two-level vegetation-herbivore trophic system. We describe the dynamics of this species using the Hutchinson equation

$$(3.7) \quad \dot{V}(t) = a_1 V(t) \left(1 - \frac{V(t - \tau)}{K} \right),$$

where τ reflects the time needed for recovery of vegetation from being grazed. It is well known (see e.g. [4]) that the Hutchinson equation has a positive steady state $V^* = K$ which is stable for $\tau < \pi/(2a_1) = \tau_{\text{crit}}$, loses stability at τ_{crit} and is unstable for larger τ . This means that the delay in (3.7) yields stability or instability depending on its proportion to the characteristic growth-rate time $T = 1/a_1$ of the system.

Now, we add the next species to our ecosystem increasing the trophic level and considering the vegetation-herbivore-carnivore system described by the Hutchinson equation coupled with the predator equation. Therefore, the model reads

$$(3.8) \quad \begin{cases} \dot{V}(t) = a_1 V(t) \left(1 - \frac{V(t - \tau)}{K} \right) - b_1 V(t) P(t), \\ \dot{P}(t) = -a_2 P(t) + b_2 V(t) P(t). \end{cases}$$

In [9] it is claimed that for such systems there are three characteristic times: τ and T described above and \tilde{T} which is the geometric mean of herbivore birth and carnivore death times which reflects the characteristic period for prey-predator oscillations in Lotka-Volterra system (see e.g. [10]). Typically, we have $T < \tau < \tilde{T}$ and this yields stability.

Now, we check stability switches for (V^*, P^*) as a steady state of (3.8). For this system the characteristic matrix reads

$$\begin{pmatrix} -a_1 \frac{V^*}{K} e^{-\lambda\tau} - \lambda & -b_1 V^* \\ b_2 P^* & -\lambda \end{pmatrix},$$

which leads to the characteristic function

$$W(\lambda) = \lambda^2 + b_1 b_2 V^* P^* + \frac{a_1 V^*}{K} \lambda e^{-\lambda\tau} = \lambda^2 + c_2 + c_1 \lambda e^{-\lambda\tau}.$$

We easily calculate the auxiliary function

$$f(y) = y^2 - (2c_2 + c_1^2)y + c_2^2$$

and see that $f(y) = 0$ (that is, $g(\sqrt{y}) = 0$) has two positive solutions

$$\bar{y}_1 = \frac{2c_2 + c_1^2 - c_1 \sqrt{c_1^2 + 4c_2}}{2} \quad \text{and} \quad \bar{y}_2 = \frac{2c_2 + c_1^2 + c_1 \sqrt{c_1^2 + 4c_2}}{2} > \bar{y}_1.$$

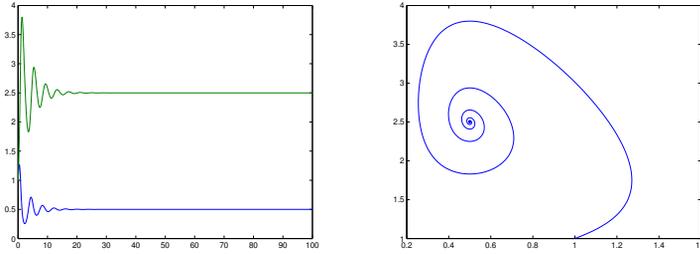


Fig. 7. Plot of solution to (3.8) for $\tau = 0.1$

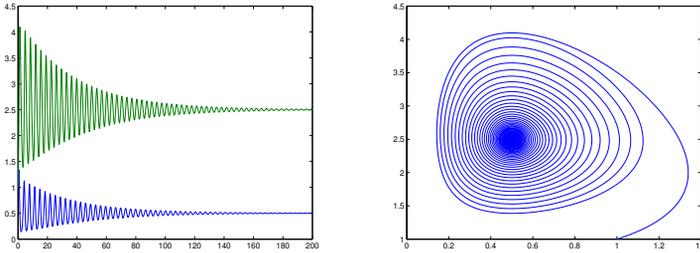


Fig. 8. Plot of solution to (3.8) for $\tau = 0.8$

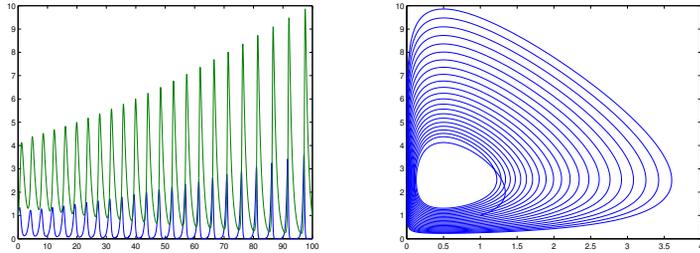


Fig. 9. Plot of solution to (3.8) for $\tau = 0.9$

It is obvious that $f'(\bar{y}_1) < 0$ and $f'(\bar{y}_2) > 0$. In this case we have two sequences of critical delays τ_k^1 and τ_k^2 for which $i\omega_1$ and $i\omega_2$, $\bar{\omega}_i = \sqrt{y_i}$, are the eigenvalues, respectively. The identity $W(i\bar{\omega}) = 0$ yields $\bar{\omega}_1\tau_k^1 = \pi/2 + 2k\pi$ and $\bar{\omega}_2\tau_k^2 = \pi/2 + 2k\pi$. Let us consider τ_0^1 and τ_0^2 . The inequality $\bar{\omega}_1 < \bar{\omega}_2$ implies $\tau_0^1 > \tau_0^2$. Therefore, if τ increases starting from $\tau = 0$, the first critical value of delay for which (V^*, P^*) can lose stability is τ_0^2 . For this critical delay there is a pair of purely imaginary eigenvalues $\pm i\bar{\omega}_2$ and the Main Theorem shows that the eigenvalues at τ_0^2 cross the imaginary axis from left to right so that (V^*, P^*) loses stability. As τ increases, the next critical value of delay can be either τ_0^1 or τ_1^2 depending on the model parameters. More precisely, if $\bar{\omega}_2 < 6\bar{\omega}_1$, then $\tau_0^1 < \tau_1^2$ and then the next critical delay is τ_0^1 for which the eigenvalues cross the imaginary axis from right to left and (V^*, P^*) can

gain stability. If $\bar{\omega}_2 > 6\bar{\omega}_1$, then $\tau_0^1 > \tau_1^2$ and then the next critical delay is τ_1^2 for which the eigenvalues cross the imaginary axis from left to right and (V^*, P^*) stays unstable. With increasing delay, stability switches can occur under the assumption that the sequences of critical delays fulfil

$$(3.9) \quad \tau_0^2 < \tau_0^1 < \tau_1^2 < \tau_1^1 < \dots < \tau_k^2 < \tau_k^1 < \tau_{k+1}^2.$$

However, the sequences $(\tau_k^1)_{k \in \mathbb{N}}$ and $(\tau_k^2)_{k \in \mathbb{N}}$ are both arithmetic progressions with difference $2\pi/\bar{\omega}_1$ and $2\pi/\bar{\omega}_2$, respectively. Therefore, there exist $k \in \mathbb{N}$ such that (3.9) ceases to hold and then (V^*, P^*) becomes unstable. The number of possible stability switches depends on the model parameters.

4. Discussion. In this section we summarise and discuss the results presented in the previous section. As can be seen, different ecological assumptions reflected in different models with delays lead to different dynamics of resulting prey-predator systems. The most complicated behaviour depending on the model parameters is obtained for system (3.8) proposed as the description of a three-level trophic system (see [9]). In this model there is always a change of stability of the positive steady state with increasing delay. Moreover, for some parameter values there can be a finite sequence of stability switches ending with instability for large delays.

When the delay is introduced into the prey-predator interaction term the behaviour also depends on the manner of introducing the delay. If the delay is introduced into the per capita growth rate, then there is always a change of stability for some critical value of delay and there is no possibility of gaining stability again. For the system where the delay is introduced into the whole interaction term the dynamics depends on the magnitude of the carrying capacity K of prey species. More precisely, if $K < 3V^*$, then the positive steady state (V^*, P^*) is stable independently of the delay. For $K > 3V^*$ a change of stability occurs for a critical value of delay and a sequence of stability switches cannot occur.

We see that for system (3.1) with delay introduced under different ecological assumptions all three possible types of dependence on the delay are possible. These three types are the following:

- The steady state is stable independently of the delay.

This behaviour is a consequence of non-existence of purely imaginary eigenvalues, which is equivalent to non-existence of positive roots of the auxiliary function g .

- The steady state loses stability for some critical value of the delay and cannot gain it again for larger delays.

This is connected with the function g that has one positive root. For such g the function f which is a quadratic function also has one positive

root at which f is increasing. Therefore, at every critical value of delay the eigenvalues cross the imaginary axis from left to right and the number of eigenvalues with positive real parts increases. This implies that the steady state loses stability at the first critical delay and cannot gain it for larger delays.

- There is a sequence of stability switches with increasing delay which ends with instability for large delays.

This type of behaviour can occur for a system with the function g having two positive roots. If $y_1 < y_2$ are the roots of g , then $f'(y_1) < 0$ and $f'(y_2) > 0$. On the other hand, the critical values of delay depend inversely on the roots of g and hence $\tau_{\text{crit}}^1 > \tau_{\text{crit}}^2$, that is, for τ_{crit}^2 a change of stability occurs. On the other hand, for both y_1 and y_2 there is a sequence of critical values of delay at which the steady state can change stability due to the existence of purely imaginary eigenvalues. Both sequences τ_n^1 and τ_n^2 are arithmetic progressions with different differences. Therefore, there can appear a finite sequence of stability switches with increasing delay.

It should be noted that when the steady state loses stability and becomes unstable, then typically the Hopf bifurcation is observed and the system has periodic solutions oscillating around the steady state.

Finally, we would like to compare critical values of delays calculated for specific parameter values of (3.1). Assume that $a_1 = 3$, $b_1 = 0.5$, $K = 100$, $a_2 = 0.2$, $b_2 = 0.01$. For these parameter values the characteristic times mentioned by May [9] are $T = 1/a_1 = 1/3$, $\tilde{T} = \sqrt{a_1 a_2} \approx 0.77$ and $\tau_{\text{crit}} \approx 0.52$, where τ_{crit} denotes the critical delay of the Hutchinson equation where there is a change of stability in this equation. We see that $T < \tau_{\text{crit}} < \tilde{T}$, as is suggested in [9]. According to the suggestions of May the critical delay for a three-level trophic system described by the prey-predator system with delay should be significantly greater, which may reflect the well known ecological rule of increasing stability with increasing number of species involved in the ecosystem. Indeed, for these parameter values the critical values of delays are 1.428050311 for (3.8) and 1.396019183 for (3.2), respectively, while $\tau_{\text{crit}} = 0.5235987758$, which is significantly smaller.

It should also be noted that the method described in this paper obviously can also be applied in the case of a steady state which is unstable for $\tau = 0$. In such a case we can check whether this state can gain stability with increasing delay and whether stability switches are possible.

It is obvious that the three types of behaviour described above can also be observed in other delayed models with two variables and in delayed models with three or more variables, while stability switches are not possible in the case of one variable delayed models, where the auxiliary function f is linear

and it has a constant derivative yielding the movement of eigenvalues in one direction for each critical value of delay.

In general, for delayed models with two or more variables, from the Main Theorem we can deduce that

- if the auxiliary function f has no positive root, then a change of stability is not possible;
- if the auxiliary function f has exactly one positive root, then there can be exactly one change of stability from stable to unstable steady state, and if the steady state loses stability, it cannot gain it again;
- if the auxiliary function f has at least two positive roots, then stability switches with increasing delay are possible.

Acknowledgements. The results of this paper were presented at the 15th National Conference on Applications of Mathematics in Biology and Medicine (XV KKZMBM), 16th–19th September 2009, Szczyrk, Poland.

The paper was supported by Polish Ministry of Science, grant No. N N201 362536.

References

- [1] O. Arino and E. Sánchez, *Delays induced in population dynamics*, in: Mathematical Modelling of Population Dynamics, Banach Center Publ. 63, R. Rudnicki (ed.), Inst. Math., Polish Acad. Sci., Warszawa, 2004, 9–46.
- [2] K. Cooke and P. van den Driessche, *On zeroes of some transcendental equations*, Funkcial. Ekvac. 29 (1986), 77–90.
- [3] K. Cooke and Z. Grossman, *Discrete delay, distributed delay and stability switches*, J. Math. Anal. Appl. 86 (1982), 592–627.
- [4] U. Foryś, *Biological delay systems and the Mikhailov criterion of stability*, J. Biol. Systems 12 (2004), 1–16.
- [5] —, *Mathematics in Biology*, Wydawnictwa Naukowo-Techniczne, Warszawa, 2005 (in Polish).
- [6] J. K. Hale and S. M. Verduyn Lunel, *Introduction to Functional Differential Equations*, Springer, New York, 1993.
- [7] N. D. Hayes, *Roots of the transcendental equation associated with a certain difference-differential equation*, J. London Math. Soc. 25 (1950), 226–232.
- [8] G. E. Hutchinson, *Circular casual systems in ecology*, Ann. New York Acad. Sci. 50 (1948), 221–246.
- [9] R. M. May, *Time-delay versus stability in population models with two or three trophic levels*, Ecology 54 (1973), 315–325.
- [10] J. D. Murray, *Mathematical Biology I: An Introduction*, Springer, 2001.
- [11] J. Skonieczna and U. Foryś, *Stability switches for some class of delayed population models*, in: Proc. 15th National Conference on Mathematics Applied in Biology and Medicine, Silesian Technical Univ., 2009.
- [12] P. J. Wangersky and W. J. Cunningham, *Time lag in prey-predator population models*, Ecology 38 (1957), 136–139.

Joanna Skonieczna, Urszula Foryś
Institute of Applied Mathematics
Faculty of Mathematics, Informatics and Mechanics
University of Warsaw
Banacha 2
02-097 Warszawa, Poland
E-mail: js222152@students.mimuw.edu.pl
urszula@mimuw.edu.pl

*Received on 17.5.2010;
revised version on 13.1.2011*

(2048)