JOURNAL OF DIFFERENTIAL EQUATIONS **152**, 394–408 (1999)
Article ID jdeq.1998.3533, available online at http://www.idealibrary.com on IDEAL®

# Stability Loss Delay in Harvesting Competing Populations

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Received December 17, 1997; revised June 29, 1998

When populations are in competition, it often happens that one of them disappears. Harvesting may be used for the control and management of competing species to stabilize the populations at a persistent equilibrium. A three-dimensional model, where the harvesting effort is a dynamic variable, is studied in the case where the growth rate of the harvesting effort is very slow. The analysis shows that the system can have relaxation oscillations. Dynamic bifurcation theory is used to determine the maximal and minimal values of harvesting effort along this cycle of oscillations. © 1999 Academic Press

*Key Words:* dynamical systems; singular perturbation; competing species; dynamic bifurcations; delayed loss of stability; cycles.

## 1. INTRODUCTION

Stability loss delay in dynamical bifurcations is an important and newly discovered phenomenon. Consider a system of differential equations $x' = f(x, y)$, $x \in D \subset \mathbf{R}^n$, depending on a real parameter $y$. Suppose that for each fixed value of the parameter, the system has an equilibrium point $x = \xi(y)$, continuously depending on $y$. Suppose also that there exists a bifurcational value $y = y_*$ for the parameter, at which the equilibrium loses stability, that is, $x = \xi(y)$ is a stable equilibrium for $y < y_*$, and unstable for $y > y_*$. Suppose now that the parameter $y$ is a slowly varying dynamical variable,

* Supported by the National Sciences and Engineering Research Council of Canada.
† Supported by the GdR "Outils et Modèles de l'Automatique pour la Dynamique des Ecosystèmes et le Contrôle des Resources Renouvelables," C.N.R.S.



0022-0396/99 $30.00

that is, $y' = \varepsilon g(x, y)$, where $\varepsilon > 0$ is small, and that $y$ passes through the bifurcational value $y_*$. The solution of system

$$x' = f(x, y)$$
$$y' = \varepsilon g(x, y) \tag{1}$$

starting at initial point $x(0) = x^0$, $y(0) = y^0 < y_*$, will go quickly near the equilibrium $x = \xi(y^0)$ and then remains close to the curve $x = \xi(y)$, until $y$ reaches some value $y^1 > y_*$, that is, the loss of stability which must occur at $y = y_*$ is delayed until $y = y^1$.

This phonemenon was first described in 1973 by Shishkova [19] in a model example. The general theory due to Neishtadt [15] appeared only in 1985. Independently, Lobry and Wallet [13], motivated by numerical experiments and the theory of canard solutions (see the appendix of this paper), insisted on the problem of dynamical bifurcation in 1986 and were among the first to recognize its importance for applications. The reader may consult [1, p. 179] and [10, 12] for more references and information on the subject. In this paper, we study the delayed loss of stability in harvesting competing populations. We note that the general theory of Neishtadt does not apply in our problem. This theory requires that a pair of eigenvalues crosses the imaginary axis, when in our case a real eigenvalue crosses zero.

Consider two competing populations $x$ and $y$. An external resource is assumed to exist that support the two populations. However, each population interferes with the use of resource by the other population. We suppose that the competition leads to the extinction of one of the two populations, say $y$. This is not a desired but an extremely frequent situation. It appears already in Volterra's original study which was inspired by observing fish populations in the Upper Adriatic. If we are interested by the control and management of competing species we may think that harvesting on the surviving population could stabilize the system at a persistent equilibrium at which both species survive.

Clark (see [3, p. 323]) studied harvesting on one of the populations in the Gause's model of interspecific competition. He observed that there is no value of the harvesting effort that leads to persistent equilibria. Thus he suggested to consider the harvesting effort as a dynamic variable. He obtained a three dimensional system, that he analyzed in the case where the dynamics of the harvesting effort is very slow, compared to the dynamics of the two populations. He detected a "pseudo-limit cycle" behavior and he noticed that the system does not necessarily undergo precise limit-cycle oscillations. However his discussion uses only a *static bifurcation* analysis, in a problem which requires a *dynamic bifurcation* analysis. In particular, the important phenomenon of the delayed loss of stability of equilibria is not examined, so the minimal and maximal values of the harvesting effort along the cycle, proposed by Clark, are false. The delayed loss of stability had not been always fully understood in the literature. It led some authors to errors and confusion (see [2, 11] for details and references).

In this paper, the equations of growth of the two populations are more general than Gause's model. We consider the model problem

$$\begin{aligned} x' &= xM(x, y, E), \\ y' &= yN(x, y), \\ E' &= \varepsilon EP(x), \end{aligned} \tag{2}$$

where $x$ and $y$ are two competing populations and $E$ is a harvesting effort. We show that, under suitable hypotheses, the system exhibits an "exact cycle" of oscillations, not only a "pseudo-limit cycle" behavior. We approximate the size of this cycle. This paper is organized as follows. In Section 2, we give particular attention to the Gause's model. In Section 3, we describe the two competing species model and we analyze the effect of harvesting on one of the two populations. In Section 4, we consider the effort of harvesting as a dynamic variable and we analyze the three dimensional differential system using Tikhonov's theory. In Section 5, we study the dynamical bifurcations occurring in the system and the delayed loss of stability of equilibria and we describe the cycle of oscillations. In the Appendix, we carry out numerical experiments, we recall the main result of Tikhonov's theory, and we give some comments on canard solutions.

## 2. CLARK'S ANALYSIS OF GAUSE'S MODEL

Hereafter we consider the Gause's model of interspecific competition, based on the equations

$$\begin{aligned} x' &= rx(1 - x/K) - \alpha xy, \\ y' &= sy(1 - y/L) - \beta xy, \end{aligned} \tag{3}$$

where $r$, $s$, $K$, $L$, $\alpha$, and $\beta$ denote positive constant and the prime $'$ denotes the derivative with respect to time. We restrict our study to the positive values of $x$ and $y$. Each population, in absence of the other population, grows following a logistic growth law. Let $\mu$ be the graph of the function $y = (r/\alpha)(1 - x/K)$, $0 \leqslant x \leqslant K$. This curve is a component of the isocline $x' = 0$. Let $\nu$ be the graph of the function $x = (s/\beta)(1 - y/L)$, $0 \leqslant y \leqslant L$. This curve is a component of the isocline $y' = 0$. We suppose that the coefficients in equation (3) satisfy the condition $1 > \alpha L/r > s/\beta K$. The only stable equilibrium is at $(K, 0)$. Thus, competition leads to the extinction of the $y$ population. Now, let the $x$ population be subject to harvesting. System (3) becomes

$$x' = rx(1 - x/K) - \alpha xy - qEx,$$
$$y' = sy(1 - y/L) - \beta xy, \qquad (4)$$

Let $\mu_E$ be the graph of the function $y = (r/\alpha)(1 - x/K) - (q/\alpha)E$, $0 \leqslant x \leqslant x_E$, where $x_E = K(1 - qE/r)$ and $0 \leqslant E \leqslant c$, $c = r/q$. This curve is a component of the isocline $x' = 0$. It moves downwards, parallel to itself, as the value of $E$ increases. Let $a < b$ be defined by

$$a = \frac{r}{q}\left(1 - \frac{\alpha L}{r}\right), \qquad b = \frac{r}{q}\left(1 - \frac{s}{\beta K}\right).$$

Apart from the equilibria $(0, 0)$ and $(0, L)$, an equilibrium exists at $(x_E, 0)$. For $0 \leqslant E < a$, all orbits except those lying on the $y$-axis (see Fig. 1.a) tend to the asymptotically stable equilibrium $(x_E, 0)$. Hence competition together with harvesting lead to the extinction of the $y$ population. For $a < E < b$, the two stable equilibria $(x_E, 0)$ and $(0, L)$ are separated by a saddle point equilibrium $S_E$, and the outcome depends on the initial populations level: Orbits tend to $(x_E, 0)$ or $(0, L)$, except for orbits lying on the stable separatrix of $S_E$ (see Fig. 1.b). Thus the equilibrium point $S_E$ makes it mathematically possible, but extremely unlikely, for both populations to survive. Hence competition together with harvesting lead to the extinction of one of the two populations. For $E > b$ all orbits except those lying on the $x$-axis (see Fig. 1.c) tend to the asymptotically stable equilibrium $(0, L)$. Hence competition together with harvesting lead to the extinction of the $x$ population. There are two bifurcational values. The first bifurcation occurs at $E = a$, for which the stable equilibrium point $(0, L)$ loses stability (for decreasing values of $E$). The second bifurcation occurs at $E = b$, for which

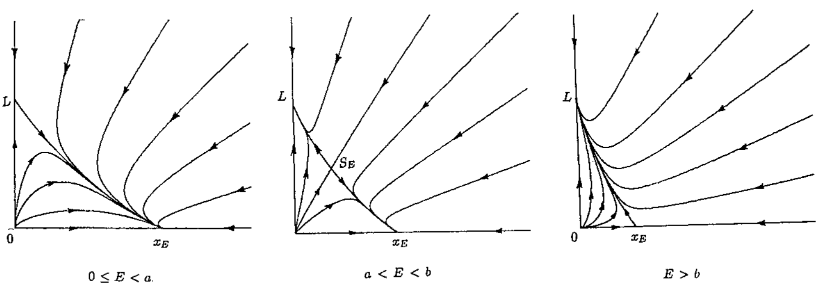


**FIG. 1.** Competing species in the Gause's model (4) with $E =$ constant. All the values of $E$ lead to the extinction of one of the two populations.

the stable equilibrium point $(x_E, 0)$ loses stability (for increasing values of $E$).

Since competition together with harvesting lead always to the extinction of one of the two populations, Clark suggested to consider effort $E$ itself as a dynamic variable that satisfies

$$E' = \varepsilon E(x - x_\infty), \tag{5}$$

where $\varepsilon$ is small, that is, the $E$ reaction occurs much more slowly than the $x$ and $y$ reactions. The component $x = x_\infty$ of the isocline $\dot{E} = 0$ is an horizontal plane. Let us assume (see Fig. 2.a) that $0 < x_\infty < x_b$, where $x_b = s/\beta$. Let $E_\infty = (r/q)(1 - x_\infty/K)$. In a heuristic analysis of system (4–5), Clark detected a "pseudo limit-cycle" behavior (see [3, Fig. 10.6]). A slow transition $AB$ develops near the slowly moving equilibrium $(x_E, 0)$, with increasing effort $E$, until the $b$ bifurcational value, where the equilibrium $(x_E, 0)$ loses its stability. Near $b$, a fast transition $BC$ leads the $x$ and $y$ populations near the stable equilibrium $(0, L)$. Then a slow transition $CD$ develops near the stable equilibrium $(0, L)$, with decreasing effort $E$, until the $a$ bifurcational value, where the equilibrium $(0, L)$ loses stability. Near $a$, a fast transition $DA$ leads the $x$ and $y$ populations near the stable equilibrium $(x_E, 0)$, closing the "pseudo-cycle" $ABCD$. This heuristic analysis does not give a good understanding of the phenomenon. In fact we prove that the system has an exact cycle of oscillations $A'B'C'D'$, not only a "pseudo limit-cycle" behavior. Moreover the actual fast transitions $B'C'$ and $D'A'$ occur near values $E_{\min}$ and $E_{\max}$ and the slow transitions $A'B'$ and $C'D'$ along equilibria $(x_E, 0)$ and $(0, L)$ develop for $E_{\min} \leqslant E \leqslant E_{\max}$,

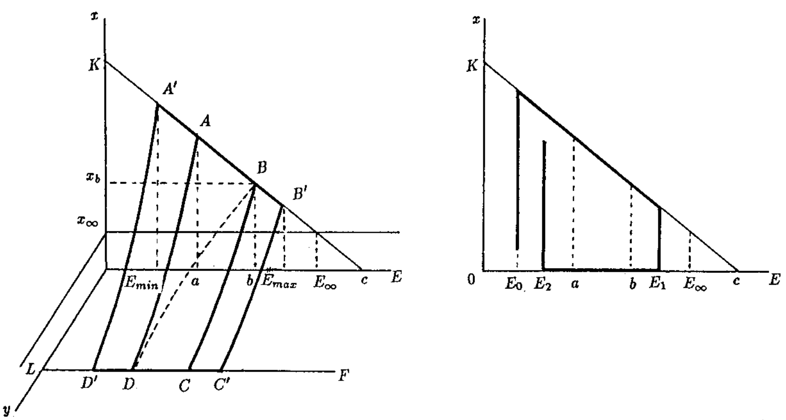


**FIG. 2.** The cycle of oscillations in the model (4–5) or (6), when the harveting effort $E$ is a slow dynamic variable. The slow transition $BB'$ (resp. $DD'$) develops near the repelling component of the slow curve $(x_E, 0)$ (resp. $(0, L)$).

but $E_{\min} < a < b < E_{\max}$. This is due to the phenomenon of delayed loss of stability in dynamical bifurcations: A delay occurs because the actual departure of an orbit from the equilibrium that has lost stability takes place not immediately afterwards, but rather after a time during which the effort $E$ changes by a finite amount. Let us explain this behavior in our more general context of system (2).

## 3. HARVESTING COMPETING SPECIES

Consider system (2). We assume that the functions $M$ $N$ and $P$ are continuous and that system (2) has a unique solution with prescribed initial conditions.We assume, following Clark, that $\varepsilon$ is small. Let us denote by $\tau$ the time in system (2). We look at the behavior of system (2) for large values of time of order $1/\varepsilon$. If we go to the time $t = \tau/\varepsilon$, we obtain the system

$$\begin{aligned} \varepsilon\dot{x} &= xM(x, y, E), \\ \varepsilon\dot{y} &= yN(x, y), \\ \dot{E} &= EP(x), \end{aligned} \tag{6}$$

where the dot denotes the derivative with respect to the new time $t$. System (6) can be analyzed with Tikhonov's theorem [20] which is the fundamental result in Singular Perturbation Theory (for the convenience of the reader, we recall this result in the Appendix). Let us apply this theorem to system (6). We restrict our attention to the positive octant. The fast equations are

$$\begin{aligned} x' &= xM(x, y, E), \\ y' &= yN(x, y), \end{aligned} \tag{7}$$

where the harvesting effort is considered as a parameter. The following assumptions are made.

1. The component $\nu = \{(x, y): N(x, y) = 0\}$ of the isocline $y' = 0$ is the graph of a nonnegative continuous map $x = n(y)$ such that $n: [0, L] \to \mathbf{R}$ and $n(L) = 0$. The function $N$ is positive to the left of the curve $\nu$ and negative to the right.

2. There exists a nonnegative continuous function $E \mapsto x_E$ defined on $[0, c]$, $c > 0$, such that $x_c = 0$. Moreover, the component $\mu_E = \{(x, y): M(x, y, E) = 0\}$ of the isocline $x' = 0$ is the graph of a nonnegative continuous map $y = m_E(x)$ such that $m_E: [0, x_E] \to \mathbf{R}$ and $m(x_E) = 0$. The function $M$ is positive below the curve $\mu_E$ and negative above it.

3. There exists $a \in ]0, c[$ such that for all $0 \leqslant E < a$, the curve $\nu$ remains above the curve $\mu_E$. There exists $b \in ]a, c[$ such the for $a \leqslant E \leqslant b$ the curves $\mu_E$ and $\nu$ intersect at point $S_E$ only and $S_a = (0, L)$, $S_b = (x_b, 0)$. Moreover, for $b < E \leqslant c$, the curve $\mu_E$ remains to the left of $\nu$.

From the above hypothesis we deduce that

$$M(0, L, a) = N(x_b, 0) = 0. \tag{8}$$

Apart from the equilibria (0, 0) and (0, $L$), an equilibrium exists at $(x_E, 0)$. We can easily prove as in Gause's model that all values of effort $E$, except when $a < E < b$ and for a small set of initial conditions, lead to the extinction of one of the two populations (see Fig. 3). Thus we have the following result.

THEOREM 1. *All values of the harvesting effort lead to the extinction of one of the two populations* (*except for a small set of initial conditions*).

We denote by $\gamma_E$ the particular trajectory of the fast equation that goes from the singular point $(0, L)$ to the singular point $(x_E, 0)$ (resp. from $(x_E, 0)$ to $(0, L)$) in case $E < a$ (resp $E > b$). There are two bifurcation values. The first bifurcation occurs at $E = a$, for which the stable equilibrium point $(0, L)$ loses stability (for decreasing values of $E$). The second bifurcation occurs at $E = b$, for which the stable equilibrium point $(x_E, 0)$ loses stability (for increasing values of $E$). Hence the slow manifold $xM(x, y, E) = 0 = yN(x, y)$ consists of many components (see Fig. 2.a) :

1. The $E$ axis which is the set of the unstable equilibria (0, 0). This component is repelling.

2. The line $LF$ which is the set of the equilibria $(0, L)$. The arc $LD$ is repelling and the arc $DF$ is attracting.

3. The arc $Kc$ which is the set of the moving equilibria $(x_E, 0)$. The arc $KB$ is attracting and the arc $Bc$ is repelling.

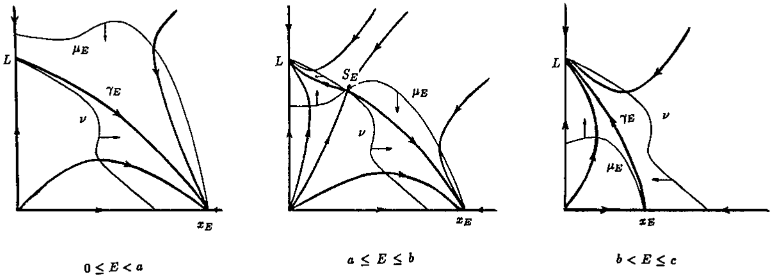


**FIG. 3.** The fast dynamics (7) for various values of the harvesting effort.

4. The arc $BD$ which is the set of the unstable equilibria $S_E$. This component is repelling.

Let us assume that there exists $x_\infty$, such that $0 < x_\infty < x_b$, $P(x_\infty) = 0$, $P > 0$ for $x > x_\infty$, and $P < 0$ for $x < x_\infty$. Let $E_\infty$ be the value of $E$ for which $x_\infty = x_E$. In Fig. 2.a, we see that the slow transition $AB$ ends at point $B$ where the equilibrium of the fast dynamics loses stability. At this point one can think, following Clark, that a new fast transition may develop until point $C$ of the attracting component $LF$ of the slow manifold. Owing to stability loss delay, the actual fast transition takes place at point $B'$, that is, the slow transition continues to develop along the repelling component $BB'$ of the slow manifold.

## 4. DELAYED LOSS OF STABILITY

Let us consider a trajectory (see Fig. 2.b which represents the projection of the trajectory on the plane $(E, x)$) of system (6) that arrives near the equilibrium near the equilibrium $(x_E, 0)$ (resp. $(0, L)$) at *entry point* $E_0 < b$ (resp. $E_1 > a$). We have already mentioned that the actual departure of this trajectory from the equilibrium takes place not immediately after $b$ (resp. after $a$) but rather after a time during which the effort $E$ changes by a finite amount. Let $E_1 > b$ (resp. $E_2 < a$) be the *exit point*. The main problem is to compute $E_1$ from $E_0$ (resp. $E_2$ from $E_1$), that is, to calculate the *entrance-exit function* along the slow curve $\{(x_E, 0, E): 0 < E < E_\infty\}$ (resp. the slow curve $\{(0, L, E): 0 < E\}$) of system (6). More precisely, let $\mathcal{T}_\delta$ be a tube of axis $x = x_E$, $y = 0$, (resp. $x = 0$, $y = L$) and radius $\delta$ where $\delta > 0$ is not too big. We consider the integral curve of (6) that starts at $(x^0, y^0, E_0)$, where $E_0 < b$ and $(x^0, y^0, E_0) \in \mathcal{T}_\delta$ (resp. at $(x^0, y^0, E_1)$, where $E_1 > a$ and $(x^0, y^0, E_1) \in \mathcal{T}_\delta$). If $\varepsilon$ is small enough, according to Tikhonov's theorem, this curve remains inside the tube $\mathcal{T}_\delta$ and goes towards the curve $x = x_E$, $y = 0$ (resp. the curve $x = 0$, $y = L$), with increasing (resp. decreasing) $E$ as long as $E < b$ (resp. $E > a$). Denote the next intersection of this curve with the tube $\mathcal{T}_\delta$ by $(x_1, y_1, p_1(E_0, \varepsilon, x^0, y^0))$ (resp. $(x_2, y_2, p_2(E_1, \varepsilon, x^0, y^0))$). Of course $x_1$ and $y_1$ (resp. $x_2$ and $y_2$) depend also on $\varepsilon$ and on the initial conditions. We are interested in $\lim_{\varepsilon \to 0} p_1(E_0, \varepsilon, x^0, y^0)$ and $\lim_{\varepsilon \to 0} p_2(E_1, \varepsilon, x^0, y^0)$. We show that these limits exist and are independent of the initial density populations for $\delta$ sufficiently small. Let $E_1$ (resp. $E_2$) such that $E_1 > b$ (resp. $E_2 < a$) and

$$\int_{E_0}^{E_1} \frac{N(x_E, 0)}{EP(x_E)}\, dE = 0 \qquad \left(\text{resp. } \int_{E_1}^{E_2} \frac{M(0, L, E)}{E}\, dE = 0\right).$$

THEOREM 2. $\lim_{\varepsilon\to 0} p_1(E_0, \varepsilon, x^0, y^0) = E_1$ *and* $\lim_{\varepsilon\to 0} p_2(E_1, \varepsilon, x^0, y^0) = E_2$.

*Proof.* Let us consider the change of variable

$$Y = \varepsilon \ln y \qquad (\text{resp. } X = \varepsilon \ln x), \tag{9}$$

which maps the strip $0 < y < 1$ (resp. $0 < x < 1$) into the half space $Y < 0$ (resp. $X < 0$). This change of variable transforms system (6) into

$$\left.\begin{aligned} \varepsilon\dot{x} &= xM(x, \exp Y/\varepsilon, E), \\ \dot{Y} &= N(x, \exp Y/\varepsilon), \\ \dot{E} &= EP(x), \end{aligned}\right\} \quad \text{resp.} \quad \left\{\begin{aligned} \dot{X} &= M(\exp X/\varepsilon, y, E), \\ \varepsilon\dot{y} &= yN(\exp X/\varepsilon, y), \\ \dot{E} &= EP(\exp X/\varepsilon), \end{aligned}\right. \tag{10}$$

when $Y < 0$, $\lim_{\varepsilon\to 0} \exp Y/\varepsilon = 0$ (resp. when $X < 0$, $\lim_{\varepsilon\to 0} \exp X/\varepsilon = 0$). The initial condition becomes $(x^0, \varepsilon \ln y^0, E_0)$ (resp. $(\varepsilon \ln x^0, y^0, E_1)$). System (10) is a slow-fast system. Its slow surface is given by equation $M(x, 0, E) = 0$, that is, $x = x_E$ (resp. by equation $N(0, y) = 0$, that is, $y = L$). According to Tikhonov's theory, $x$ (resp. $y$) varies quickly towards the stable equilibrium $x = x_E$ (resp. $y = L$). Then a slow transition develops near the surface $x = x_E$ (resp. $y = L$). This slow transition is approximated by the solution of the slow equations

$$\begin{aligned} \dot{Y} &= N(x_E, 0), \\ \dot{E} &= EP(x_E), \end{aligned} \qquad \left(\text{resp.} \quad \begin{aligned} \dot{X} &= M(0, L, E), \\ \dot{E} &= EP(0), \end{aligned}\right)$$

with initial condition $(0, E_0)$ (resp. $(0, E_1)$). Hence

$$Y(E) = \int_{E_0}^{E} \frac{N(x_E, 0)}{EP(x_E)}\, dE \qquad \left(\text{resp. } X(E) = \int_{E_1}^{E} \frac{M(0, L, E)}{EP(0)}\, dE\right).$$

The solution of the slow equations reaches again the axis $Y = 0$ (resp. $X = 0$) at value $E_1$ (resp. $E_2$). Returning to the original variables we see that the solution $(x(t, \varepsilon), y(t, \varepsilon), E(t, \varepsilon))$ crosses again the tube $\mathcal{T}_\delta$ when $E$ is asymptotically equal to $E_1$ (resp. $E_2$). ▮

Let $g$ (resp. $f$) be defined by

$$g(E) = \int \frac{N(x_E, 0)}{EP(x_E)}\, dE \qquad \left(\text{resp. } f(E) = \int \frac{M(0, L, E)}{E}\, dE\right).$$

The function $g$ (resp. $f$) is defined on $]0, E_\infty[$ (resp. $]0, +\infty[$). According to (8), it has a minimum at $b$ (resp. $a$) (see Fig. 4). It is strictly decreasing on $]0, b]$ (resp. $]0, a]$) and strictly increasing on $[b, E_\infty[$ (resp. on

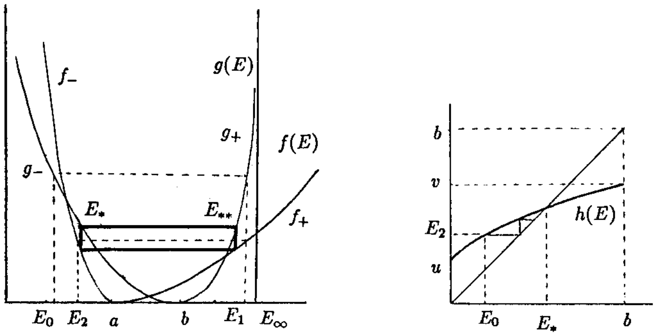


**FIG. 4.** The entrance–exit functions $g$ and $f$ along the slow curves $(x_E, 0)$ and $(0, L)$. The attracting fixed point $E_*$ of $h = f_-^{-1} \circ f_+ \circ g_+^{-1} \circ g_-$ gives rise to a cycle of oscillations.

$[a, +\infty[$ ). Let $g_-$ and $g_+$ (resp. $f_-$ and $f_+$) be the restrictions of $g$ (resp. $f$) to $]0, b]$ and $[b, E_\infty[$ (resp. $]0, a[$ and $[a, +\infty[$ ). The entrance-exit function $E_0 \mapsto E_1$ along the slow curve $x = x_E$, $y = 0$ is given by $g(E_1) = g(E_0)$, that is, $E_1 = G(E_0)$ where $G = g_+^{-1} \circ g_-$. The entrance–exit function $E_1 \mapsto E_2$ along the slow curve $x = 0$, $y = L$ is given by $f(E_2) = f(E_1)$, that is, $E_2 = F(E_1)$ where $F = f_-^{-1} \circ f_+$.

Let $\gamma(t, \varepsilon) = (x(t, \varepsilon), y(t, \varepsilon), E(t, \varepsilon))$ be a trajectory of system (6) with initial condition $(x^0, y^0, E^0)$. We assume that $E^0 \leqslant b$ and $(x^0, y^0)$ lies in the basin of attraction of the equilibrium $(x_{E^0}, 0)$ of system (7). Let $E_n$ be the sequence defined by $E_0 = E^0$ and

$$E_{2n+1} = G(E_{2n}) \qquad E_{2n+2} = F(E_{2n+1}) \qquad \text{for } n \geqslant 0.$$

We define recursively the sequences $t_n$ and $z_n(t)$ by $t_0 = 0$ and for $n \geqslant 0$,

1. $z_{2n}(t)$ is the solution of the slow equation

$$\dot{E} = EP(x_E) \qquad E(t_{2n}) = E_{2n}.$$

Then $z_{2n}(t)$ is an increasing function which reaches the value $E_{2n+1}$ at time $t_{2n+1}$.

2. $z_{2n+1}(t) = E_{2n+1} \exp P(0)(t - t_{2n+1})$ is the solution of the slow equation

$$\dot{E} = EP(0) \qquad E(t_{2n+1}) = E_{2n+1}.$$

Then $z_{2n+1}(t)$ is a decreasing function which reaches the value $E_{2n+2}$ at time $t_{2n+2}$.

Let $\bar{E}(t)$ be defined on $[0, +\infty[$ by

$$\bar{E}(t) = \begin{cases} z_{2n}(t) & \text{if} \quad t_{2n} \leqslant t \leqslant t_{2n+1}, \\ z_{2n+1}(t) & \text{if} \quad t_{2n+1} \leqslant t \leqslant t_{2n+2}. \end{cases}$$

Let $I = ]0, t_1[ \cup ]t_1, t_2[ \cup ]t_2, t_3[ \cup \cdots$ and let $\bar{x}(t)$ and $\bar{y}(t)$ be defined on $I$ by

$$\bar{x}(t) = \begin{cases} x_{\bar{E}(t)} & \text{if} \quad t_{2n} < t < t_{2n+1}, \\ 0 & \text{if} \quad t_{2n+1} < t < t_{2n+2}, \end{cases}$$

and

$$\bar{y}(t) = \begin{cases} 0 & \text{if} \quad t_{2n} < t < t_{2n+1}, \\ L & \text{if} \quad t_{2n+1} < t < t_{2n+2}. \end{cases}$$

As a consequence of Tikhonov's theorem and Theorem 2 above we have the following result.

THEOREM 3. *We have* $\lim_{\varepsilon \to 0} E(t, \varepsilon) = E(t)$ *uniformly on any compact interval* $[0, T]$. *We have also* $\lim_{\varepsilon \to 0} x(t, \varepsilon) = \bar{x}(t)$ *and* $\lim_{\varepsilon \to 0} y(t, \varepsilon) = \bar{y}(t)$ *uniformly on any compact subset of I.*

The sequence $E_{2n}$ satisfies the recurrence formula $E_{2n+2} = h(E_{2n})$ where $h$: $]0, b] \to ]0, a]$ be the mapping defined by $h = F \circ G$. The mapping $h$ is strictly increasing and maps the interval $]0, b]$ into the interval $]u, v]$ where $u = f_-^{-1} \circ f_+(E_\infty) > 0$, and $v = f_-^{-1} \circ f_+(b) < a$ (see Fig. 4). Then equation $E = h(E)$ has at least one attracting fixed point $E_*$, such that the sequence $E_{2n}$, starting near $E_*$, converges to $E_*$. Let $E_{**} = G(E_*)$. Let $\Gamma = A'B'C'D'$ be the closed curve consisting of the arcs $A'B' = \{(x_E, 0, E)$: $E_* \leqslant E \leqslant E_{**}\}$ and $C'D' = \{(0, L, E)$: $E_* \leqslant E \leqslant E_{**}\}$ and the orbits $B'C' = \gamma_{E_{**}}$ and $D'A' = \gamma_{E_*}$ of the fast dynamics (see Fig. 2). Thus we have the following result.

THEOREM 4. *There exists* $\delta > 0$ *such that for any tubular neighborhood* $\mathcal{V}$ *around* $\Gamma$, *there exist* $\varepsilon_0 > 0$ *and* $T_0 > 0$ *with the property that for* $0 < \varepsilon < \varepsilon_0$, *any solution of system* (6), *whose initial condition* $(x^0, y^0, E^0)$ *satisfies* $|E^0 - E_*| < \delta$, *will arrive, for* $t \geqslant T_0$ *inside* $\mathcal{V}$ *and never leave it.*

*Proof.* Let $\delta > 0$ be such that the sequence $E_{2n}$ defined by $E_{2n+2} = h(E_{2n})$ and $|E_0 - E_*| < \delta$ converges to $E_*$. Let $\mathcal{V}$ be a tubular neighborhood of diameter $\eta$ around $\Gamma$. There exists $n_0$ such that $|E_{2n} - E_*| < \eta/2$ for all $n \geqslant n_0$. Let $T_0 = t_{2n_0}$ and let $T > T_0$. According to Theorem 3, there exists $\varepsilon_0 > 0$ such that $|E(t, \varepsilon) - \bar{E}(t)| < \eta/2$ for all $t \in [T_0, T]$ and $\varepsilon < \varepsilon_0$.

We have also $|x(t, \varepsilon) - \bar{x}(t)| < \eta/2$ and $|y(t, \varepsilon) - \bar{y}(t)| < \eta/2$ for all $t \in [T_0, T] - J$ where $J = \bigcup J_n$ is a reunion of small intervals $J_n$ centered at $t_n$. On each interval $J_n$, the trajectory is approximated by $\gamma_{E_n}$ with an error of order $\eta/2$. Thus, the trajectory is inside $\mathscr{V}$ for all $t \in [T_0, T]$. It remains to prove that it never leaves it for $t > T$. Assume that this is false. Let $t > T$ be the smallest value such that the trajectory lies on the boundary of $\mathscr{V}$. This must happen only along the arcs $B'C'$ or $D'A'$, since along the arcs $A'B'$ or $C'D'$, the trajectories are exponentialy close to these arcs. Applying Theorem 3 we see that the trajectory was already outside $\mathscr{V}$ for some time before $t$, which contradicts the choice of time $t$. ▮

Using Brouwer fixed point theorem we conclude that system (6) has an exact cycle which lies in a small tube around $\Gamma$. Along this cycle the minimal and maximal values $E_{\min}$ and $E_{\max}$ of the harvesting effort satisfy $E_{\min} \approx E_*$ and $E_{\max} \approx E_{**}$. This cycle is not necessarily a limit cycle. In Gause's model (3), the functions $f$ and $g$ are

$$f(E) = e^{qE} E^{\alpha L - r}, \qquad g(E) = E^{s - \beta K} (E_\infty - E)^{\beta x_\infty - s},$$

and the function $h$ is strictly convex, so it has a unique fixed point which is globaly attracting. In this model all trajectories starting in the positive octant will approach $\Gamma$.

## A. APPENDIX

### A.1. *Remarks and Numerical Experiments*

Strictly speaking we did not prove that the cycle near $\Gamma$ is an attractor but only that all the solutions in a neighborhood of the cycle will arrive when $t$ is large enough in a small tube around that cycle and that the radius of the tube goes to zero with $\varepsilon$. From a practical point of view this is perhaps the same as saying that the cycle is an attractor, but it is well known that three dimensional systems may present very complex and fascinating behavior with a mixture of periodic behavior, strange attractors and chaos. So there is no reason to exclude the possible existence of a lot of distinct periodic orbits that lie in the small tube around the cycle. The description of trajectories agrees perfectly with numerical experiments (see Fig. 5). This figure is obtained in case of model (4–5) with the following values of parameters : $\varepsilon = 0.05$, $r = 2$, $K = 10$, $\alpha = 0.2$, $q = 0.2$, $s = 1$, $L = 7$, $\beta = 0.25$, $x_\infty = 2$. This figure shows the cycle of oscillation in three dimensional space and its projection in $xE$-space.

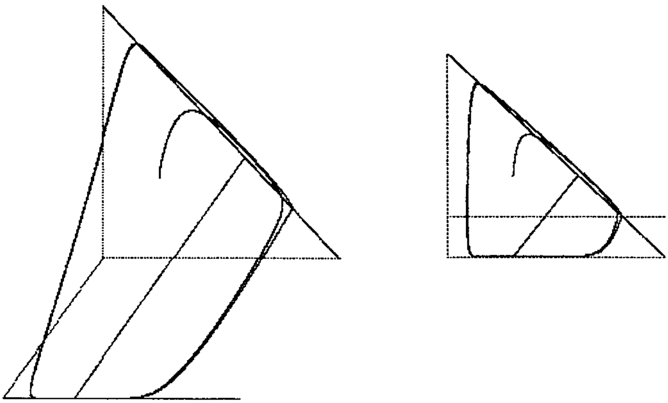

**FIG. 5.** The cycle of oscillations for the parameter values reported in the text.

## A.2. *Tikhonov's Theory*

Let us consider an initial value problem of the form

$$\begin{cases} \varepsilon\dot{x} = F(x, y, \varepsilon) & x(0) = \alpha_\varepsilon, \\ \dot{y} = G(x, y, \varepsilon) & y(0) = \beta_\varepsilon, \end{cases} \tag{11}$$

where $\dot{} = d/dt$, $x \in \mathbf{R}^n$, $y \in \mathbf{R}^m$ and $\varepsilon$ is a positive real parameter. We look at the solutions behavior when $\varepsilon$ is small. The small parameter $\varepsilon$ is multiplying the derivative, and so the usual theory of continuous dependence of the solutions with respect to the parameters cannot be applied. According to Tikhonov's theory, first $x$ varies very quickly and is approximated by the solution of the *boundary layer equation*

$$x' = F(x, \beta_0, 0) \qquad x(0) = \alpha_0, \tag{12}$$

and $y$ remains close to its initial value $\beta_0$. The system of differential equations

$$x' = F(x, y, 0), \tag{13}$$

in which $y$ is a parameter, is called the *fast equation*. Assume that the solutions of (13) tend towards an equilibrium $\xi(y)$, where $x = \xi(y)$ is a root of equation

$$F(x, y, 0) = 0. \tag{14}$$

The manifold $\mathscr{L}$ of equation (14) is called the *slow manifold*: It is the set of equilibrium points of the fast equation (13). The surface of equation $x = \xi(y)$ is a component of the slow manifold. The solution of (12) is defined for all $\tau \geqslant 0$ and tends to $(\xi(\beta_0), \beta_0)$, namely to a point of the slow manifold $\mathscr{L}$.

Hence a fast transition brings the solution of problem (11) near the slow manifold. Then, a slow motion takes place near the slow manifold, and is approximated by the solution of the *reduced problem* (or *slow equation*)

$$\dot{y} = G(\xi(y), y, 0) \qquad y(0) = \beta_0. \tag{15}$$

The preceding description is definitely heuristic and imprecise. In a more rigorous description we usually consider $\varepsilon$ as a parameter that tends to 0 and we assume that problem (11) has a unique solution $x(t, \varepsilon)$, $y(t, \varepsilon)$. Let $y_0(t)$ be the solution of the reduced problem (15), which is assumed to be defined for $0 \leqslant t \leqslant T$, then we have

$$\lim_{\varepsilon \to 0} y(t, \varepsilon) = y_0(t), \qquad \text{for} \quad 0 \leqslant t \leqslant T.$$

We have also $\lim_{\varepsilon \to 0} x(t, \varepsilon) = \xi(y_0(t))$, but the limit holds only for $0 < t \leqslant T$, since there is a boundary layer at $t = 0$, for the $x$-component. Indeed, let $x_0(\tau)$ be the solution of the boundary layer equation (12), then $\lim_{\varepsilon \to 0} x(\varepsilon\tau, \varepsilon) = x_0(\tau)$ for $0 \leqslant \tau < +\infty$. This description of the solution of problem (11) was given by Tikhonov [20], under the hypothesis that the equilibrium point $\xi(y)$ of equation (13) is asymptotically stable for all $y$ and that the asymptotic stability is uniform with respect to $y$. See also [6, 8, 9, 16, 21].

### A.3. *Canards*

System (1) is a fast-slow system and its trajectories are described by the Tikhonov theory as long as the bifurcational value $y_*$ is not reached. The stability loss delay phenomenon fits the theory of *canards* which are trajectories of fast and slow systems that moves for a long time along the unstable part of the slow manifold $f(x, y) = 0$, after having moved for a long time along the stable part of the slow manifold. Canards solutions were first rigorously studied in 1978 by a group of French mathematicians, namely E. Benoît, J. L. Callot, F. Diener, and M. Diener (see [4, 17, 22] for complete references), using Nonstandard Analysis. We have also to our disposal standard studies of the French canards [5, 7, 14]. Rigorous proofs (using standard analysis) in a two dimensional system were given also by Schecter [18] in 1985. The logarithmic change of variables (9), which is the fundamental tool in our study, appeared first in the nonstandard literature on the subject.

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