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Stabilization of an oscillating n-dimensional structured population model

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Abstract— **We consider a model of a predator with q size-classes feeding on one resource. The resource is also modelled by a logistic function. This model may have sustained oscillations in dimension (q+1) around an unstable equilibrium. A possible control consists in harvesting every class. We show that (under good assumptions) this model can be reduced to a two-dimensional predator-prey model having sustained oscillations. We design positive controls to suppress the oscillations and to stabilize the equilibrium of the reduced and full model.**

I. INTRODUCTION

Size-structured models are often used in biological modelling because they allow more realism in the described phenomena. In population dynamics, the structure can be age, size or even any physiological parameter that plays an important role in the behaviour of individuals [16]. The problem is that the number of state variables increases and that the dynamics become complex and difficult to study. Such models may exhibit several stable equilibria, oscillations, chaos. But, often, man may act on these systems, via harvesting for example. An important problem is to use this action (this control in the language of Control Theory, see [14]) to try to (for example) stabilize the system toward a desired equilibrium. The problem is not simple, and was rarely addressed in the literature, because the biological origin of the problem brings some specificity: for example, very often, the control (or harvesting) is positive, and cannot be negative. Mathematically, that makes the problem more difficult, even in the linear case ([3]). Moreover, the models are in general **not** linear.

In this work, we consider such a problem and give some techniques to obtain results. The model is a classical prey-predator model where the predator is structured with q size classes or stages. The control is the harvesting on these classes. Without control, the system has a limit-cycle in the $(q+1)$ dimensional space (as we show). With a positive control u, we are able to stabilize at least locally the trajectories around the equilibrium.

For general results about harvesting in a biological population, see [4] where the results are given only at the equilibrium. For biological models of population with discrete classes and control, see [12], but the model does not have limit cycles. For similar techniques of structured models without control, see [1]. For positive linear control, see [3], [13]. For similar problems, see [5], [10].

We describe the model in a first section, then reduce it and control it. The work is illustrated with numerical simulations.

II. THE POPULATION MODEL WITH q SIZE CLASSES

The model we study is rather classical : it has one resource (or prey) described by its total biomass R, and a predator structured with q size classes. Each class is measured by the number $N_i, i = 1 \dots q$ of individuals in it. The mean mass of individuals of the class i is m_i. The predator only feeds on the resource R. The energy (biomass) acquired from predation allows individuals to grow from a size class to the next except for the final class. The last class (corresponding to adults) uses acquired energy to lay eggs which become individuals of the first class when they hatch.

We assume as in [1] that the functional responses used to model predation have the following classical form ([8]):

$$f_i(R) = d_i f(R)$$

where the function $f(R)$ will be the usual saturation function

$$f(R) = \frac{R}{R_h + R} \tag{1}$$

and the coefficients d_i correspond to the maximum ingestion rate of individuals of the class i.

The passage from class i to class $i+1$ conserves the number of individuals and the biomass of the system. It is done with a rate:

$$\beta_i f_i(R) = \beta_i d_i f(R) \qquad \text{with} \qquad \beta_i = \frac{k_a}{m_{i+1} - m_i}$$

$k_a \in]0; 1]$ being the efficiency in biomass conversion. We model in a similar way the reproduction with biomass conservation and so the amount of hatching eggs is the following:

$$\alpha f_q(R) \qquad \text{with} \qquad \alpha = \frac{\epsilon k_a}{m_1}$$

ϵ corresponds to the proportion of laid eggs that hatch.

The growth of the prey is logistic with function Φ:

$$\Phi(R) = eR\left(1 - \frac{R}{K_c}\right) \tag{2}$$

where as usual e is the intrinsic growth rate and K_c the carrying capacity.

Finally, all classes of predators have a constant and identical linear death rate μ and a linear harvesting with rate $u(t)$.

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The whole model is (the notation $< . >$ denotes the scalar product between two vectors):

$$\begin{aligned}
&\dot{R} = \Phi(R) - f(R) < d, N > \\
&\dot{N}_1 = \alpha f(R) d_q N_q - \beta_1 f(R) d_1 N_1 - \mu N_1 - u(t) N_1 \\
&\dot{N}_i = \beta_{i-1} f(R) d_{i-1} N_{i-1} - \beta_i f(R) d_i N_i - \mu N_i - u(t) N_i \\
&\qquad\qquad 2 \leq i \leq q-1 \\
&\dot{N}_q = \beta_{q-1} f(R) d_{q-1} N_{q-1} - \mu N_q - u(t) N_q
\end{aligned} \tag{3}$$

The predator's dynamics can be written in a matrix form:

$$\dot{N} = f(R) A N - \mu N - u(t) N \tag{4}$$

with matrix $A \in \mathcal{M}_q(\mathbb{R})$ defined as:

$$A = \begin{pmatrix}
-\beta_1 d_1 & & & & \alpha d_q \\
\beta_1 d_1 & -\beta_2 d_2 & & & \\
& \ddots & \ddots & & \\
& & \beta_{q-2} d_{q-2} & -\beta_{q-1} d_{q-1} & \\
& & & \beta_{q-1} d_{q-1} & 0
\end{pmatrix}$$

We can show that for a positive initial condition, trajectories remain in a bounded domain of ${\mathbb{R}_+^*}^{q+1}$. Moreover this model admits two trivial equilibria $R = N_1 = \dots N_q = 0$ and $R = K_c, N_1 = \dots N_q = 0$. In the following section, we will reduce this model to a two-dimensional one and show that actually this model has under some conditions one positive equilibrium. Numerical simulations show that this equilibrium can be unstable and that the model has a limit cycle in the $(q+1)$ dimensional space. We will design the positive control u in order to stabilise this equilibrium.

III. REDUCTION OF THE MODEL

A. The limit behaviour

We consider new variables which are some proportions of the N_i. Let us introduce the vector $\gamma \in {\mathbb{R}_+^*}^q$ and the new variable

$$X = \frac{N}{< \gamma, N >} \tag{5}$$

We remark that $< \gamma, X >= 1$. The dynamics of X are:

$$\dot{X} = \frac{\dot{N}}{< \gamma, N >} - \frac{< \gamma, \dot{N} >}{< \gamma, N >} X$$

Using (4) it follows:

$$\dot{X} = f(R) \left(A X - \frac{< A^t \gamma, N >}{< \gamma, N >} X \right) \tag{6}$$

Both matrix A and A^t have the same eigenvalues. Moreover these matrix are cooperative and irreducible and so, using Perron-Frobenius theorem (see e.g. [2]), their common eigenvalue with the greatest real part is real and simple and its corresponding eigenvector is positive. Let λ be this real eigenvalue and v and w the corresponding positive eigenvector of A and A^t. Since v is positive, it is easy to check with A that λ is positive. Choosing $\gamma = w$ in (6), it follows

$$\dot{X} = f(R) \big(A - \lambda I \big) X \tag{7}$$

If $u(t) >$ constant $> -\mu$ then R can not converge to 0. If it was the case, N would also decrease to 0 while the Jacobian matrix associated to this zero equilibrium has a positive real eigenvalue $\Phi'(0)$ which makes it unstable. So there is a contradiction. Consequently the term $f(R)$ in (7) is like a change in time scale and the asymptotic behaviour of the system is given by the matrix $A - \lambda I$. We have to study a linear system. Its eigenvalues are all with negative real part except 0 that is a simple one associated to the positive eigenvector v. It follows that X will align with the line Vect(v). Since $< w, X >= 1$, we have

$$\lim_{t \to +\infty} X(t) = v^* := \frac{v}{< w, v >}$$

Denote $P(t) =< w, N(t) >$, we deduce from (5) that

$$N(t) \underset{t \to \infty}{\longrightarrow} P(t) v^*$$

The idea is now to study the limit system, i.e. when $N(t) = P(t) v^*$. It is the following classical 2-dimensional Rosenzweig-MacArthur model (see e.g. [8]):

$$\begin{aligned}
&\dot{R} = \Phi(R) - C f(R) P(t) \\
&\dot{P} = f(R) \lambda P(t) - \mu P(t) - u(t) P(t)
\end{aligned} \tag{8}$$

with $C =< d, v^* >$ and $\lambda > 0$.

Since u will be taken in a feedback form (i.e. $u(t) = u(R(t), P(t))$), it follows from this previous study the following proposition:

Proposition 1: The possible asymptotic behaviours of the $q{+}1$ dimensional system introduced in section II are the same as the possible asymptotic behaviour of the limit model (8).

Remark 1: This previous proposition follows from asymptotically autonomous system theorem (see [15]). Nevertheless we have to take care if there are many possible ω-limit sets in (8): depending on the initial condition of the $q+1$ system, we cannot predict a-priori which limit behaviour the system will have.

To illustrate this result, we have done a simulation with three size classes for the predator. On Fig.1, we have plotted the evolution of the amount of prey and the condensed predators variable $P(t) =< w, N(t) >$. On the z-axis is plotted the distance $d(N, v^*)$ between $N(t)$ and $Vect(v^*)$. We can see the convergence of the original system to the 2-dimensional limit system.

B. Classical results

There are lots of studies on this model for $u(t) = 0$ (see e.g. [7]). Let us recall the main ones:

This model always admits two trivial equilibria $E_{0i}^* = (0, 0)$ and $E_0^* = (0, K_c)$. Moreover If $f(K_c) > \mu / \lambda$, it admits a positive equilibrium E^* satisfying

$$R^* = f^{-1}\left(\frac{\mu}{\lambda}\right) \qquad \text{and} \qquad P^* = \frac{\Phi(R^*)}{C f(R^*)}$$

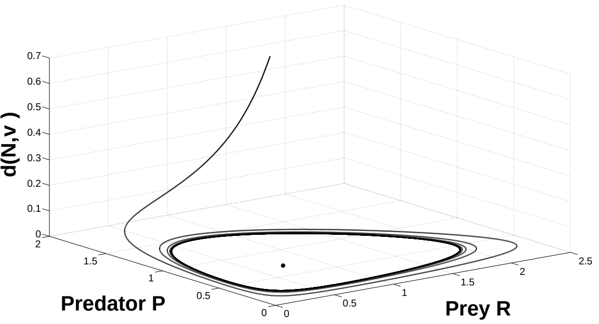


Fig. 1: Convergence of the original model to the limit model in dimension two.

When there is a positive equilibrium, E_{0i}^* and E_0^* are unstable and E^* is asymptotically locally stable if and only if:

$$\frac{d}{dR}\left(\frac{\Phi}{f}\right)(R^*) < 0 \tag{9}$$

In fact, using the Poincaré-Bendixon theorem, two asymptotic behaviours can appear: Either there is convergence to the positive equilibrium (possible only under the sufficient condition (9)) or convergence to a limit cycle.

For the choice of functions we made (1,2) this result can be specified as following (see [9]): there is existence of a positive equilibrium E^* if and only if $\mu < \mu_{\max} := K_c\lambda/(K_c + R_h)$ and we have

$$R^*(\mu) = \frac{\mu R_h}{\lambda - \mu} \tag{10}$$

Under this existence hypothesis:

i) E^* is globally stable under the condition

$$\mu \geq \mu_{\text{crit}} := \lambda\frac{K_c - R_h}{K_c + R_h}$$

ii) E^* is unstable and there is an unique limit cycle which is stable under the condition $\mu < \mu_{\text{crit}}$.

In the second case the limit cycle is the $\omega-$limit set of every starting point in ${\mathbb{R}_+^*}^2 \backslash E^*$. Moreover we know by the study of the vector field direction that the rotation is counterclockwise.

IV. ADDING A CONTROL

A. Objectives

In this section we will assume that there is existence of a positive equilibrium that is unstable without control (i.e. when $u(t) = 0$). So we are in the following situation:

(H1) $$0 < \mu < \mu_{\text{crit}} < \mu_{\max}$$

A positive control $u(t)$ corresponds to kill (or to harvest depending on what we are modelling) a fraction of the predators. A negative control corresponds to inject predators in the system proportionally to the predators still in it. The injection of predators is for example often used in biological pest control (see e.g. [6], [11]). We will assume in this section that we can control the system only with one of these two ways and so $u(t)$ will have to keep a constant sign. We will work with $u > 0$ but the following results can easily be extended to $u < 0$.

First we can notice that for a positive control, we can easily obtain a globally stable positive equilibrium taking a constant control u such as:

$$\mu_{\text{crit}} \leq \mu + u < \mu_{\max}$$

That is not our interest here because we want to minimize the amount of prey R which is an increasing function of u (see (10)). Our objective will be here to keep the current equilibrium and to stabilize it. Moreover we assume that we can observe the state variables and so the control will be as following:

$$u(t) = u\big(R(t), P(t)\big) \tag{11}$$

So we require that $u(R^*, P^*) = 0$.

Lemma 1: The positive equilibrium of system (8) is not stabilizable with a differentiable control of type (11).

Proof: To keep the current equilibrium, it is required that $u(R^*, P^*) = 0$. For a differential control u, the local stability of the equilibrium is given by the eigenvalues of the Jacobian matrix

$$J = \begin{pmatrix} \Phi'(R^*) - Cf'(R^*)P^* & -Cf(R^*) \\ \lambda f'(R^*)P^* - \frac{\partial u(R^*,P^*)}{\partial R}P^* & -\frac{\partial u(R^*,P^*)}{\partial P}P^* \end{pmatrix}$$

Since we have supposed that the equilibrium is not stable without control i.e. that $\Phi'(R^*) - Cf'(R^*)P^* > 0$, a necessary condition to stabilize the equilibrium is then:

$$0 < C\left(\frac{\Phi'(R^*)f(R^*)}{\Phi(R^*)} - f'(R^*)\right) < \frac{\partial}{\partial P}u(R^*, P^*)$$

It follows that on every neighbourhood of E^*, u has to take both negative and positive values. So we can not stabilize the equilibrium with a differentiable control. ■

In the two following sections, we will propose two non-differentiable non-negative controls to stabilize E^*. A first one depending only on the predators quantity, the second one depending on the amount of preys and predators. Nevertheless results obtained can easily be generalised to non-positive control.

B. Local positive control depending on the predators

In this section the (continuous) control will be on the form:

$$u\big(P(t)\big) = \nu \max\big(0, P(t) - P^*\big) \tag{12}$$

More precisely we will apply a positive control only in the domain $\mathcal{D}^+ := \{(R,P) : P \geq P^*\}$ and do nothing in the domain $\mathcal{D}^- := \{(R,P) : P \leq P^*\}$.

Remark 2: With such a control, it is not excluded to create other equilibria (as we can see on simulation Fig.3d). Since we will study the local stability of E^*, we will not focus on this possibility.

Theorem 1: Under the hypothesis (H1), the equilibrium E^* is locally controllable with the non-negative control defined in (12) if and only if

$$\left(\left(\frac{\Phi}{f}\right)'(R^*)\right)^2 < \lambda\frac{f'(R^*)\Phi(R^*)}{\big(f(R^*)\big)^2} \tag{13}$$

Proof: The Jacobian matrix of this system is clearly not defined when $P = P^*$, and particularly at the equilibrium point. In order to study the local stability, we will work on restrictions of the system to both sub-domain $\mathcal{D}^+$ and $\mathcal{D}^-$.
As we say in the last section, the equilibrium of the model without control being unstable, the Jacobian matrix restricted to $\mathcal{D}^-$ of the controlled model at the equilibrium point has two complex conjugate eigenvalues $a \pm ib$ with $a, b > 0$. Since the generated rotation movement is counterclockwise, we can define at least locally an input-output map from $(R_{in}, P^*) \in \{(R, P^*) : R > R^*\}$ to $(R_{out}, P^*) \in \{(R, P^*) : R < R^*\}$. It follows the local result:

$$|R_{out} - R^*| \underset{R^*}{\sim} e^{\frac{a\pi}{b}} |R_{in} - R^*| \tag{14}$$

The Jacobian matrix restricted to $\mathcal{D}^+$ of the controlled model at the equilibrium point is:

$$J_c = \begin{pmatrix} \Phi'(R^*) - Cf'(R^*)P^* & -Cf(R^*) \\ \lambda f'(R^*)P^* & -\frac{d}{dP}u(R^*, P^*)P^* \end{pmatrix}$$

It is clear that a necessary condition to stabilize the equilibrium is that the eigenvalues of J_c need to have a negative reel part. Nevertheless it is not sufficient. Two main possibilities can occur:

If the eigenvalues are real negative and distinct, we have immediately the local stability of the equilibrium. A trajectory starting in a neighbourhood of E^* in $\mathcal{D}^-$ will eventually enter $\mathcal{D}^+$ in a neighbourhood of E^* as we see in (14). Since J_c has two negative eigenvalues, E^* is attractive in this sub-domain. Moreover there is at least one stable manifold (at least locally) in $\mathcal{D}^+$ that can not be crossed by the trajectory.

If the eigenvalues are complex conjugate $a' \pm ib'$ with $a' < 0$ and $b' > 0$. Once again, they will give birth to counterclockwise rotation trajectories around E^* in $\mathcal{D}^+$. We can define locally a contraction input-output map satisfying:

$$|R_{out} - R^*| \underset{R^*}{\sim} e^{\frac{a'\pi}{b'}} |R_{in} - R^*| \tag{15}$$

Combining both (14) and (15) it follows that the resulting input-output mapping will be a contraction and so E^* locally stable if and only if:

$$e^{\frac{a\pi}{b}} e^{\frac{a'\pi}{b'}} < 1 \quad \Longleftrightarrow \quad \frac{a}{b} < -\frac{a'}{b'}$$

That is more restrictive that being in the complex half plane with negative real part. It is a cone inside this half plane such that the argument of the eigenvalues are in $]\pi - \arctan(b/a); \pi + \arctan(b/a)[$ (see Fig.2 for a graphical representation).

We will now show that under the condition (13) it is possible to choose ν such that one of these two previous conditions is satisfied. The characteristic polynomial of J_c is:

$$\begin{aligned} P_\nu(r) =& r^2 + \big(-\Phi'(R^*) + Cf'(R^*)P^* + \nu P^*\big)r \\ &+ \big(Cf(R^*)\lambda f'(R^*)P^* - \nu P^*\big(\Phi'(R^*) - Cf'(R^*)P^*\big)\big) \end{aligned}$$

The discriminant of this polynomial equation is (as a function of ν) a polynomial of degree two:

$$\begin{aligned} \Delta(\nu) =& \big(-\Phi'(R^*) + Cf'(R^*)P^* + \nu P^*\big)^2 \\ &- 4\big(Cf(R^*)\lambda f'(R^*)P^* - \nu P^*\big(\Phi'(R^*) - Cf'(R^*)P^*\big)\big) \end{aligned}$$

And the sum of the eigenvalues is:

$$S(\nu) = \Phi'(R^*) - Cf'(R^*)P^* - \nu P^*$$

We know that without control i.e. when $\nu = 0$, the eigenvalues are complex with positive real parts and so $\Delta(0) < 0$ and $S(0) > 0$. Since Δ is a polynomial of degree two in ν, it follows that there exists $\nu_\Delta > 0$ such that $\Delta(\nu_\Delta) = 0$ (corresponding to a root of multiplicity two). Moreover, since S is a decreasing function it exists $\nu_S > 0$ such that $S(\nu_S) = 0$. Assume that:

$$\nu_S < \nu_\Delta \quad \Longleftrightarrow \quad \Delta(\nu_S) < 0 \tag{16}$$

Then we have:

- if $\nu < \nu_S$: roots of P_ν are complex with positive real parts.
- if $\nu = \nu_S$: roots of P_ν are imaginary conjugate.
- if $\nu \in]\nu_S; \nu_\Delta[$: roots of P_ν complex with negative real parts.
- if $\nu = \nu_\Delta$: roots of P_ν is double and negative.

Moreover the determinant of J_c is positive then negative, it follows that there exist $\nu_{\max}$ such that:

- if $\nu \in]\nu_\Delta; \nu_{\max}[$: roots of P_ν are negative and distinct.

Finally, it exists $\nu_{\min} \in]\nu_S; \nu_\Delta[$ such that for all $\nu \in]\nu_{\min}; \nu_{\max}[$, roots of P_ν are in the cone of controllability.
In order to obtain (13), it suffices to solve analytically $\Delta(\nu_S) < 0$ using relations at the equilibrium point. ■
Simulations has been done to illustrate this results. In Fig.2 is plotted the evolution of the eigenvalues of J_c as a function of ν. Fig.3 illustrate the different behaviours the system can have depending on ν.

C. Local positive control depending on the two variables

In this section, we build a general positive feedback control of the form

$$u(R, P) = \mathrm{Max}(0, \mathrm{k_1(R - R^*) + k_2(P - P^*)}) \tag{17}$$

where k_1, k_2 are two gains to be chosen. This feedback is nonnegative, continuous, but not differentiable around (R^*, P^*). We will show that it is possible to choose the gains that stabilize the linearized system around the equilibrium.

Theorem 2: The equilibrium of system (8) can be locally stabilized by a positive feedback control of type (17).

Proof: To obtain this result, we will first prove that the linearized system around the equilibrium is controllable.

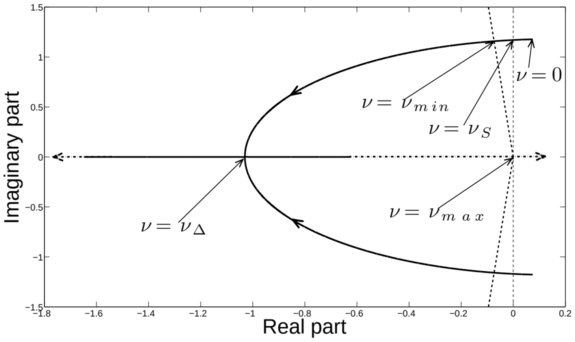
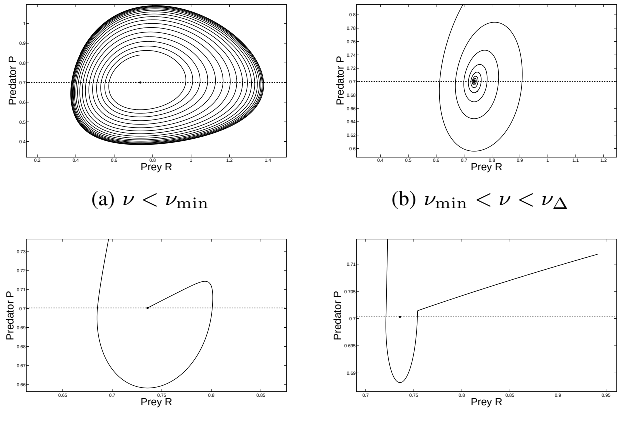


Fig. 2: Evolution of the eigenvalues of J_c in function of ν when the condition (13) is satisfied. They eventually enter the cone of controllability and we can stabilize the equilibrium for all $\nu \in]\nu_{\min}; \nu_{\max}[$.



(a) $\nu < \nu_{\min}$

(b) $\nu_{\min} < \nu < \nu_\Delta$

(c) $\nu_\Delta < \nu < \nu_{\max}$

(d) $\nu_{\max} < \nu$

Fig. 3: Different behaviours of the system depending on the value of ν. In Fig.3a, the eigenvalues of J_c are complex with negative real part and nevertheless it is not sufficient to stabilize the equilibrium. In Fig.3b eigenvalues are complex but in the cone of controllability. In Fig.3c after one passage in $\mathcal{D}^-$ (the domain under the dotted line) there is convergence to E^* after entering again $\mathcal{D}^+$. If the value of ν is too high (Fig.3d) this equilibrium becomes unstable. The simulation shows that another equilibrium appears which is stable.

Then we will show that we can choose k_1, k_2 such that the feedback control (17) stabilizes the equilibrium.

First we recall the original result from [13] for local controllability with positive controls. The system is a linear system with one input in the form

$$\dot{x} = Jx + bu \tag{18}$$

The system (18) with controls $u(.)$ belonging to the non-negative bounded measurable functions of $\mathbb{R}^+ \to [0, 1]$ is locally controllable at the origin if and only if

i) all eigenvalues of J have nonzero imaginary parts, and
ii) the controllability matrix for (18) has full rank.

Intuitively, this result says that in the uncontrolled part $u = 0$, the system rotates around the equilibrium, and thus exits the region to enter the controlled region.

In our case, matrix

$$J = \begin{pmatrix} \Phi'(R^*) - Cf'(R^*)P^* & -Cf(R^*) \\ \lambda f'(R^*)P^* & 0 \end{pmatrix}$$

and vector $b = (0, -P^*)^T$, and therefore it is clear that matrix $[b, Jb]$ has rank two. Moreover, matrix J has non zero imaginary parts, as it is easy to compute, and as it is clear from the signs of the vector field in the phase portrait around the equilibrium. Therefore the theorem applies, and the system is locally controllable to the equilibrium.

Now we have to build the controller. We choose the form (17), in an approach very similar to that of [17]. The system we consider is a kind of hybrid system, with two modes $u = 0$ and $u = k_1(R - R^*) + k_2(P - P^*)$. The system switches between these two modes along the straight line $k_1(R - R^*) + k_2(P - P^*) = 0$, that separates the plane between two half-planes. First we remark that the control is continuous along the switching boundary, so there will be no sliding modes. If a trajectory starts in the part $u = 0$, there is no control, and it will rotate until it enters the other region. In this region, because of the controllability of the system, we are able to place the eigenvalues of the closed system with the gains k_1, k_2. We choose two real distinct negative eigenvalues. Then in the controlled region there will be two half straight lines, corresponding to the two stable vector spaces. Therefore the trajectory coming from the uncontrolled part will stay in the controlled part and converges to the equilibrium, because the invariant stable eigenspaces delimitate invariant and stable regions. Finally we obtain the stability of the controlled equilibrium with this positive feedback. ■

To illustrate this result, in Fig.4 is plotted a trajectory of the unreduced system in dimension three i.e. with two size classes for the predator corresponding for example to larvae and adults. There is convergence to the limit cycle whereas the controlled system stabilizes the equilibrium.

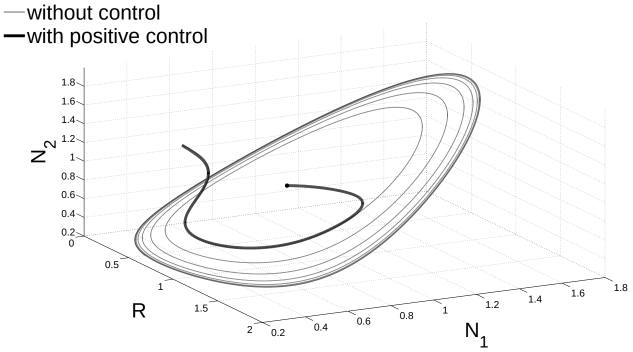


Fig. 4: Local stabilization of the equilibrium with a positive control depending on R and $< w, N >$. Trajectories are the same at the beginning because the control is 0 in this domain.

V. CONCLUDING REMARKS

The model we have studied in this paper was a prey-predator model with size-structure for the predator. To study it, we have reduced it to a two dimensional model. A rather strong hypothesis was made to allow the reduction: all classes have the same mortality rate. For a practical illustration, one could think of a bioreactor where μ is the dilution rate (the same for all classes). Nevertheless the structural stability of the results obtained allow us to get the same conclusion for small enough changes in mortality rates.

The aim of this study was to conclude that we can impose the stability of the equilibrium with a constant sign control. In practice we can not necessary build a control that may have both positive and negative values. In fishery, the control is positive whereas in biological pest control, it is negative because predators are added in the ecosystem.

The stability results obtained here are local. Nevertheless simulations seem to show that if the control does not create another positive equilibrium, the stability may be global. The study of the global stability is the aim of a current work.

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