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Biological control of parasites on orange plantations – A predator-prey model.

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Abstract

In this thesis, a four dimensional autonomous dynamical system, proposed as a model for biological control of a parasite on citrus plantations, is studied. The model is the same as that studied by Sotomayor et. al. in [1], where the system is found to have four equilibrium points, of which one exhibits a Hopf bifurcation, and a bifurcation curve is found.

In this thesis, we review and complement the work of Sotomayor et. al. [1], by proving the existence of an invariant set (volume) in the first orthant, though not for proposed parameter values. Furthermore the set is shown to be dissipative, that is, the phase fluids inside the invariant set is contracted to one of measure zero.

Then the dynamics of the normal form is compared numerically to those of the full system near the bifurcation point, for fixed parameter values.

Contents

Preface and Acknowledgement

This thesis in applied dynamical systems, concludes a five year master course in Environmental Physics and Renewable Energy at the Norwegian University of Life Sciences in Ås, Norway.

It has been a somewhat daunting task, but with the patient guidance and creative spark of my thesis advisor, Prof. John Wyller, the problems were split into more manageable pieces, and eventually solutions started to emerge.

Introduction

The citrus leafminer parasite (Phyllocnistis Citrella), gets its name from the tunnelling work its larvae do on the foliage of the trees it infests. Though not an immediate threat to the life of the plant, the larvae eat away parts of the leaves, reducing crop value and yield.

The female lays the eggs on the back of young leaves, and only rarely, under heavy infestation, on older foliage. Older plants will then be less affected, and an infestation can result in little to no change in growth or fruit yield. On younger plants an infestation can cause stagnated growth, and reduced crop yield, but is rarely fatal to the plant [17].

Insectisides are not generally recommended when managing a leafminer infestation, since the larvae resides inside the leaves where it is protected from the chemical, and can even have the adverse affect of removing its natural enemies, like the parasitic wasps *Cirrospilus* and *Pnigalio* and the predator *Galeopsomyia fausta*. As in the article [1], we assume the latter species as a biological control agent.

The use of parasitoids and predators (or entomopathogenic fungi) for biological control is nothing new, but only one out of six attempts at introducing an exotic agent for biological control, results in full control of the pest infestation [18].

For a concise introduction to the use of and history of biological control agents in Brasil, see for instance [19]. The article also confirms the issues we faced with regards to the language barrier.

This thesis sets out to prove that in the model put forth in [1], there exists an invariant set where the system is dissipative, though not for the proposed parameter values. Secondly, we study how well the truncated *normal form* approximates the the full system near a bifurcation point in phase space.

In section 1, entitled *The Model*, we introduces the model, and to some extent justify the system of equations as a model for biological control. The presentation is by no means complete, but is intended to give a feel for what the model is all about.

Section 2 (*Analysis*) is devided into four subsections;

In section 2.1 (*Preliminary Observations*) we mention the well-posedness of the system, and present some of the findings of [1] relevant to the next sections.

Section 2.2 (*Invariant set*)[1], we define the set in phase space invariant to the flow of the model system.

In section 2.3 (*Normal Form*) we derive an expression for the normal form based on the article of Crawford [15], and try to make the connection with the method presented in [1].

Finally, in section 2.4 (*Numerical Simulations*), we compare the result of the normal form with those of the original system near the bifurcation point. The simulations of this section (as well as the verification of the results in section 2.1) were conducted with the use of SageMath [13].

[1]This section was significantly reduced and hastily reassembled, when a mistake was spotted shortly before the deadline. Hopefully all mistakes have now been weeded out.

1 The Model

A study of the citrus leafminer parasite on orange plantations in Brazil has been carried out with the use of a system of differential equations given by [1]

$$\begin{aligned} P' &= \phi_1(1 - \frac{M}{c_1})M - (\alpha_1 + \beta_1)P - k_1PG \\ M' &= \alpha_1 P - \mu_1 M \\ L' &= \phi_2(1 - \frac{G}{c_2})G - (\alpha_2 + \beta_2)L + k_2PG \\ G' &= \alpha_2 L - \mu_2 G. \end{aligned} \tag{1}$$

The parasite in question is the citrus leafminer (*Phyllocnistis Citrella*) which, at its larva stage, is a serious pest in parts of the agricultural industry. Their natural enemy, the *Galeopsomyia fausta*, will at its larva stage, consume the pupae of the leafminer. Adhering to the notation of [1] and using the same assumptions on the parameters, the list of system variables are:

P measures the pupa population of the leaf miner (the prey)

M measures the adult leaf miners population

L measures the larva of the *Galeopsomyia fausta* population (the predator)

G measures the adult population of *Galeopsomyia fausta*.

Suggested parameter values are restated here for convenience. The biological justification of these values is beyond the scope of this thesis, and the capabilities of the author, but can be found in [24] (in Portuguese).

$\alpha_1 = 0.7$	$\beta_1 = 0.003$	$\mu_1 = 0.6$	$\phi_1 = 2.3$	$c_1 = 400000$
$\alpha_2 = 0.3$	$\beta_2 = 0.00015$	$\mu_2 = 0.4$	$\phi_2 = 4$	$c_2 = 100$

Table 1: Suggested parameter values taken from [1]

The system of equations (1) together with the proposed parameter values of Table 1, models infestations of citrus plantations in Brazil, by the citrus leafminer. This is a compartmentalized model where each compartment (equation) represents one or more stages in the evolution of the leafminer parasite and their natural enemy. This particular system was originally presented in [22, 23, 24]. The equations describe the "flux" balance in and out of the compartments. At its simplest form the model equation for such systems reads,

$$\frac{dx_i}{dt} = Q^i_{in} - Q^i_{out}$$

from which some of the assumptions made when the model was formulated, can be inferred. Table 2 sorts the parameters by their effect on the flux on each compartment.

Var	IN	OUT	Description
P	ϕ_1		Birth rate of the species (at pre-adult stage)
		c_1	Carrying capacity of species.
		α_1	Rate at which the species evolves to its adult stage.
		β_1	Death rate of the pre-adult stage.
		k_1	Factor measuring the rate at which the species get eaten. (proportional to number of encounters)
M	α_1		Rate at which the species evolves to its adult stage.
		μ_1	Death rate of the species (adult stage).
L	ϕ_2		Birth rate of the species (at pre-adult stage)
	k_2		Factor measuring the rate at which the species eats. (proportional to number of encounters)
		c_2	Carrying capacity of species.
		α_2	Rate at which the species evolves to its adult stage.
		β_2	Death rate of the pre-adult stage.
G	α_2		Rate at which the species evolves into its adult stage.
		μ_2	Death rate of the species (adult stage).

Table 2: Parameter Table, (see [1] for more details)

Remark
Another approach to modeling evolutionary stages is to introduce a delay that could account for the stages of evolution of little biological interest, which in this scenario would be the adult stages, where the species are neither parasites, predators nor prey.

The reader familiar with the Lotka-Volterra model,

$$\begin{aligned} \frac{dX}{dt} &= X(a - bY) \\ \frac{dY}{dt} &= Y(cX - d) \end{aligned} \tag{2}$$

will probably note some clear similarities with (1). In [2] though, it is pointed out that the Lotka-Volterra model is structurally unstable, that is, small perturbation of the system have profound effects on the type of phase portrait one gets, which is unfortunate for a model for biological control. Also issues of the exponential growth of the prey, in absence of predators is mentioned, and a solution is proposed, namely to incorporate a logistic growth terms, similar to:

$$\begin{aligned} \frac{dX}{dt} &= X(r_1(1 - \frac{X}{c_1}) - b_1Y) \\ \frac{dY}{dt} &= Y f(X, Y) \end{aligned} \tag{3}$$

Different candidate function are also proposed for $f(X, Y)$ in [2], but if one chooses $f(X, Y) = r_2(1 - \frac{Y}{c_2}) + b_2X$, the system reads:

$$\begin{aligned}\frac{dX}{dt} &= X(r_1(1-\frac{X}{c_1}) - b_1Y)\\ \frac{dY}{dt} &= Y(r_2(1-\frac{Y}{c_2}) + b_2X)\end{aligned} \tag{4}$$

Adding a terms that accounts for the mortality rate of the species, yields;

$$\begin{aligned}\frac{dX}{dt} &= X(r_1(1-\frac{X}{c_1}) - d_1 - b_1Y)\\ \frac{dY}{dt} &= Y(r_2(1-\frac{Y}{c_2}) - d_2 + b_2X)\end{aligned} \tag{5}$$

Now by separating the stages of evolution of both predator and prey population, one can deduce model (1). It should be mentioned that more involved models have been proposed and studied in [23, 24].

The model is formulated such that all the parameters are assumed to be positive. Furthermore, any equilibrium of the system at negative variable values will be ignored for obvious reasons.

Remark

From a biological point of view, it makes sense to add the condition $k_2 \leq k_1$. This is equivalent to assuming the "cost" of loosing one member of the prey population is greater than the "reward" for the predators.

In [1] an analysis of one of the systems four equilibrium points is conducted. There is only one such point that is not in the region where two or more of the compartments are empty (extinct), giving it a particular significance. The Hopf bifurcation that occurs as the parameters (k_1 and k_2) are varied, is then studied by changing the carrying capacity parameter c_2, which is said to be of biological interest, since it represents multiple factors.

2 Analysis

2.1 Preliminary Observations

In this section we mostly restates the preliminary results of [1] that are relevant for the next sections.

The first thing to note is that system (1) has a well defined (total) derivative. The vector field $\underline{f}$ of (1) is given by:

$$\frac{d\underline{x}}{dt} = \begin{bmatrix} P' \\ M' \\ L' \\ G' \end{bmatrix} = \begin{bmatrix} \phi_1(1-\frac{M}{c_1})M - (\alpha_1+\beta_1)P - k_1PG \\ \alpha_1 P - \mu_1 M \\ \phi_2(1-\frac{G}{c_2})G - (\alpha_2+\beta_2)L + k_2PG \\ \alpha_2 L - \mu_2 G \end{bmatrix} \equiv \underline{f}(\underline{x}). \tag{6}$$

The Jacobian matrix A of the vector field $\underline{f}$ is given by

$$A = \frac{\partial \underline{f}}{\partial \underline{x}} = \begin{pmatrix} -Gk_1 - \alpha_1 - \beta_1 & \phi_1 - \frac{2M\phi_1}{c_1} & 0 & -Pk_1 \\ \alpha_1 & -\mu_1 & 0 & 0 \\ Gk_2 & 0 & -\alpha_2 - \beta_2 & Pk_2 - \frac{(2G-c_2)\phi_2}{c_2} \\ 0 & 0 & \alpha_2 & -\mu_2 \end{pmatrix}$$

which elements are defined and continuous for all $\underline{x} \in \mathbb{R}^4$. Hence $\underline{f}$ is continuously differentiable, and the system of equations is well posed by the Picard's existence and uniqueness theorem, which merely requires Lipschitz continuity.

As in [1], the expression for the equilibrium points are simplified by introducing the dimensionless variables:

$$R_1 = \frac{\alpha_1\phi_1}{\mu_1(\alpha_1+\beta_1)}$$
$$R_2 = \frac{\alpha_2\phi_2}{\mu_2(\alpha_2+\beta_2)}$$

Feeding the system to a computer, and substituting for R_1 and R_2 yields the following expressions for the equilibrium solutions (with $\underline{A}_n = (P_n, M_n, L_n, G_n)$):

$$\underline{A}_1 = [0,0,0,0]$$
$$\underline{A}_2 = \left[\frac{c_1\mu_1}{\alpha_1}\left(1-\frac{1}{R_1}\right), c_1\left(1-\frac{1}{R_1}\right), 0, 0\right]$$
$$\underline{A}_3 = \left[0, 0, \frac{c_2\mu_2}{\alpha_2}\left(1-\frac{1}{R_2}\right), c_2\left(1-\frac{1}{R_2}\right)\right]$$

These equilibrium points all contain two or more zeros, meaning at least two compartments are empty. Of the three, the points $\underline{A}_3$ and $\underline{A}_1$ are clearly the most promising, since here the leaf miners are extinct. As stated in the article [1], these points are hyperbolic (saddle points), which means their local behavior is readily deduced by their linearization, and are of little interest here.

The fourth equilibrium point ($\underline{A_4}$), which experiences the Hopf bifurcation, is given by the lengthy component expressions:

$$\begin{aligned}
P_4 &= \frac{c_1\mu_1\phi_2}{\alpha_1^2\phi_1\phi_2 + \mu_1^2 c_1 c_2 k_1 k_2}\left(\phi_1\alpha_1\left(1-\frac{1}{R_1}\right) - \mu_1 c_2 k_1\left(1-\frac{1}{R_2}\right)\right)\\
M_4 &= \frac{c_1\alpha_1\phi_2}{\alpha_1^2\phi_1\phi_2 + \mu_1^2 c_1 c_2 k_1 k_2}\left(\alpha_1\phi_1\left(1-\frac{1}{R_1}\right) - \mu_1 c_2 k_1\left(1-\frac{1}{R_2}\right)\right)\\
L_4 &= \frac{c_2\mu_2\alpha_1\phi_1}{\alpha_2\alpha_1^2\phi_1\phi_2 + \alpha_2\mu_1^2 c_1 c_2 k_1 k_2}\left(c_1 k_2\mu_1\left(1-\frac{1}{R_1}\right) + \phi_2\alpha_1\left(1-\frac{1}{R_2}\right)\right)\\
G_4 &= \frac{c_2\alpha_1\phi_1}{\alpha_1^2\phi_1\phi_2 + \mu_1^2 c_1 c_2 k_1 k_2}\left(c_1\mu_1 k_2\left(1-\frac{1}{R_1}\right) + \alpha_1\phi_2\left(1-\frac{1}{R_2}\right)\right).
\end{aligned} \tag{7}$$

Here, as in [1], sufficient conditions to ensure that all the equilibrium points are located in the positive orthant are assumed, that is:

$$\begin{aligned}
&R_1, R_2 \geq 1\\
&k_1 \quad \leq \frac{\alpha_1\phi_1}{\mu_1 c_2}\frac{\left(1-\frac{1}{R_1}\right)}{\left(1-\frac{1}{R_2}\right)} \equiv k_{1,max}
\end{aligned} \tag{8}$$

2.2 Invariant set

The first main goal of this article is to show the existence of an invariant set $\Sigma \subset \mathbb{R}^4$ with only positive coordinate values. The existence assumes some additional conditions on the parameters, which will be listed in the proposition. If these conditions are biologically feasible, is unknown to the author.

Since the set Σ should reside in the positive region of $\mathbb{R}^4$, a natural place to start is considering the flux of the system over the boundaries of the first *orthant* in $\mathbb{R}^4$, (ie. $\{(i,j,k,l)|\quad i,j,k,l \geq 0\}$), where the flux is given by the vector field $\underline{f}$ in (6). Introducing the hyperplanes $(P,M,L,0),(P,M,0,G),(P,0,L,G),(0,M,L,G)$ with outward directed unit normal vectors $n_{G=0} = (0,0,0,-1), n_{L=0} = (0,0,-1,0), n_{M=0} = (0,-1,0,0), n_{P=0} = (-1,0,0,0)$ respectively, one finds the "outward" flux over these surfaces is given by:

$$\begin{aligned}
\underline{f}\cdot n_{P=0} &= \phi_1\left(\frac{M}{c_1}-1\right)M\\
\underline{f}\cdot n_{M=0} &= -\alpha_1 P\\
\underline{f}\cdot n_{L=0} &= \phi_2\left(\frac{G}{c_2}-1\right)G - k_2 PG\\
\underline{f}\cdot n_{G=0} &= -\alpha_2 L
\end{aligned}$$

The set Σ is clearly invariant with respect to the flow (ϕ^t) defined by the model, if there is no outward flux. This imposes the conditions:

$$P \geq 0, \quad 0 \leq M \leq c_1, \quad L \geq 0, \quad 0 \leq G \leq c_2 \tag{9}$$

Remark

Note that the necessary conditions are more relaxed, by allowing $0 \leq G \leq c_2 + \frac{k_2 P}{\phi_2} c_2$, *but even though* $\frac{k_2 P}{\phi_2} c_2$ *could grow large, for simplicity we opt for a box shape here.*

Now the goal is to find the other four hyperplanes enclosing the volume element Σ, satisfying these conditions and restricting the flux in positive M and G directions. To this end introduce the planes $(p, M, L, G), (P, m, L, G), (P, M, l, G), (P, M, L, g)$ where $p, m, l, g \in \mathbb{R}^+$ are constants to be determined. The unit normal vectors are given by $n_{P=p} = (1, 0, 0, 0), n_{M=m} = (0, 1, 0, 0), n_{L=l} = (0, 0, 1, 0), n_{G=g} = (0, 0, 0, 1)$ respectively, ant the flux over these planes is given by;

$$\begin{aligned}
\underline{f} \cdot n_{P=p} &= \phi_1 \left(1 - \frac{M}{c_1}\right) M - (\alpha_1 + \beta_1) p - k_1 p G \\
\underline{f} \cdot n_{M=m} &= \alpha_1 P - \mu_1 m \\
\underline{f} \cdot n_{L=l} &= \phi_2 \left(1 - \frac{G}{c_2}\right) G - (\alpha_2 + \beta_2) l + k_2 P G \\
\underline{f} \cdot n_{G=g} &= \alpha_2 L - \mu_2 g
\end{aligned} \tag{10}$$

From (10), two new conditions can be appended to (9):

$$\frac{\alpha_1 p}{\mu_1} \leq m \leq c_1, \qquad \frac{\alpha_2 l}{\mu_2} \leq g \leq c_2. \tag{11}$$

These take care of the flux over the surfaces (P, m, L, G) and (P, M, L, g) respectively. Checking the flux over the remaining two planes is now unavoidable, since we need to limit the growth of the variable L and P. From now on, we will assume the above inequality to be an equality, so as to try to maximize to volume of Σ. This has an effect on the range of admissible parameter values (see the remark below). Starting with the plane $P = p$ (first equation in (10)):

$$\begin{aligned}
\underline{f} \cdot n_{P=p} &= \phi_1 \left(1 - \frac{M}{c_1}\right) M - (\alpha_1 + \beta_1) p - k_1 p G \\
&\leq \frac{\phi_1 c_1}{4} - (\alpha_1 + \beta_1) p - k_1 p G \\
&\leq \frac{\phi_1 c_1}{4} - (\alpha_1 + \beta_1) p \\
&= \frac{\phi_1 c_1}{4} - (\alpha_1 + \beta_1) \frac{\mu_1 m}{\alpha_1} \\
&= \frac{\phi_1 c_1}{4} - (\alpha_1 + \beta_1) \frac{\mu_1 m \phi_1}{\alpha \phi_1} \\
&= \frac{\phi_1 c_1}{4} - \frac{m \phi_1}{R_1} \leq 0
\end{aligned}$$

which gives a more tangible condition on m and p given by $m \geq \frac{R_1 c_1}{4}$. In the above expressions the fact that $M \to M - \frac{M^2}{c}$ on the interval $[0, c]$, has a maximum at $\frac{c}{2}$ given by $\frac{c}{4}$, was exploited. G was tacitly assumed to be positive.

Applying the same procedure on the last hyperplane, accounting for the flux along the positive L direction, out of Σ, yields:

$$\begin{aligned}
\underline{f} \cdot n_{L=l} &= \phi_2 \left(1 - \frac{G}{c_2}\right) G - (\alpha_2 + \beta_2) l + k_2 P G \\
&\leq \frac{\phi_2 c_2}{4} - (\alpha_2 + \beta_2) l + k_2 P G \\
&= \frac{\phi_2 c_2}{4} - (\alpha_2 + \beta_2) \frac{\mu_2 g}{\alpha_2} + k_2 P G \\
&= \frac{\phi_2 c_2}{4} - \frac{\phi_2 g}{R_2} + k_2 P G \\
&\leq \frac{\phi_2 c_2}{4} - \frac{\phi_2 g}{R_2} + k_2 \frac{\mu_1 m}{\alpha_1} g \leq 0
\end{aligned}$$

Since we will choose $m = c_1$ to maximize the volume, and since all parameters and values are again assumed to be positive, this can be written as a condition on g given by;

$$\frac{\phi_2 c_2}{4} \leq \left[\frac{\phi_2}{R_2} - \frac{k_2 \mu_1 c_1}{\alpha_1}\right] g \qquad \rightarrow \qquad R_2 \leq \frac{\phi_2 \alpha_1}{k_2 \mu_1 c_1} \Bigg\} \qquad \text{bracket must be positive}$$

$$\frac{\phi_2 c_2}{4\left[\frac{\phi_2}{R_2} - \frac{k_2 \mu_1 c_1}{\alpha_1}\right]} \leq g \leq c_2$$

This finally gives an expressions for the values p, m, l, and g and the eight sides of the box Σ have now been determined. These results are summarized in the following proposition.

Proposition 1
If the parameters of system (1)*, in addition to conditions* (8) *also satisfy the conditions:*

$$\begin{aligned}
R_1 &\leq 4 \\
R_2 &\leq \frac{4\phi_2 \alpha_1}{\phi_2 \alpha_1 + 4 k_2 \mu_1 c_1}
\end{aligned} \tag{12}$$

then there exists a 4-cell Σ*, invariant with respect to the flow of system (1) given by:*

$$\Sigma = \{(P, M, L, G) | \quad 0 \leq P \leq \frac{c_1 \mu_1}{\alpha_1}, \quad 0 \leq M \leq c_1, \quad 0 \leq L \leq \frac{c_2 \mu_2}{\alpha_2}, \quad 0 \leq G \leq c_2\} \tag{13}$$

The conditions in Proposition 1 arise from the requirement that the interval of valid m and g values be non-empty (ie. $\frac{R_1 c_1}{4} \leq \frac{\alpha_1 p}{\mu_1} = m \leq c_1$ yields the first condition, etc). Unfortunately these conditions are not satisfied by proposed parameter values presented in the article [1].

Remark (1)
Initial values chosen in the interior of Σ *will stay in the interior of* Σ*. This means that, by this model, species may only approach extinction inside* Σ*.*

Remark (2)
Explicitly the four equations (10) *with equations* (9) *generate the minimum conditions;*

$$\frac{R_1 c_1}{4} \leq \frac{\alpha_1 p}{\mu_1} \leq m \leq c_1$$
$$\frac{\alpha_2 l}{\mu_2} \leq g \leq c_2$$
$$\frac{\phi_2 c_2}{4} - \frac{\phi_2 \alpha_2}{\mu_2 R_2} l + k_2 p g \leq 0.$$

This shows that the choice of p, m, l *and* g *has an effect on the accepted parameter values. Unfortunately, with the suggested parameter values, even if one minimizes* p *and* g*, then maximizes* l*, the parameters still need to satisfy the inequality;*

$$k_2 \leq \frac{4\phi_2 \alpha_1}{R_1 R_2 \mu_1 c_1} \approx 1.23e^{-6}$$

which is far from the bifurcation curve. On the bifurcation curve, k_2 *reaches a minimum at around* $k_2 \approx 3e^{-3}$ *[1].*

The bottleneck is finding a hyperplane restricting the flow in the positive L *direction, that is, in the direction of increasing density of larvae of Galeopsomyia fausta (the predator).*

Proposition 2
Any volume of initial conditions $\Omega_0 \subset \Sigma$ *is contracted to to a set of measure zero at a rate given by* $-(\alpha_1 + \alpha_2 + \beta_1 + \beta_2 + \mu_1 + \mu_2) - k_1 G$

Proof *The proposition follows directly from corollary 2.1 in appendix F, which gives the change in volume with respect to time;*
$\frac{dV}{dt} = \int_{\Omega(t)} \nabla \cdot (\underline{f}) d\underline{x}$
Here $\underline{f}$ *is given by* (6). □

2.3 Normal Form

The process for deriving the normal form employed in the article of Sotomayor et. al. [1], adds several layers of abstractions to the basic approach (some of which are presented in the appendices) by means of what is called the Poincare's method. This has the benefit of simplifying the notation. In addition the algorithms derived in [11] are easily incorporated into the approach. For our purposes, though, it is more convenient to derive the normal form without these added complexities. The goal being to emphasize traits of the process relevant to the next section, where the reduced system is compared with the original.

There are several approaches to constructing normal forms with or without bifurcation parameters in the mix. In [3], center manifold reduction, and the *method of multiple scales* is used, while in [15, 20, 21, 9] all use different, but somewhat overlapping approaches, though the latter of which deals specifically with hypernormal forms (see remark below).

In the next section, in addition to using the parameters of Table 2, we fix the parameter vector $\underline{\alpha} = \binom{k_1}{k_2}$, and deduce a simpler expression for the system in phase space. The system behavior near the bifurcation point, where a limit cycle is generated, will then not be visible, since this cycle can be thought of as having a zero radius at the bifurcation curve [15]. The justification for using the center manifold theory close to (but not on) the bifurcation curve, follows form the study of the suspended system;

$$\begin{aligned} P' &= \phi_1(1 - \frac{M}{c_1})M - (\alpha_1 + \beta_1)P - k_1PG \\ M' &= \alpha_1 P - \mu_1 M \\ L' &= \phi_2(1 - \frac{G}{c_2})G - (\alpha_2 + \beta_2)L + k_2PG \\ G' &= \alpha_2 L - \mu_2 G \\ k_1' &= 0 \\ k_2' &= 0 \end{aligned} \tag{14}$$

(with a center manifold now parameterized by $h = h(k_1, k_2, \underline{x}_c)$). Here a topological normal form exhibiting a limit cycle appears, for parameter values close to the bifurcation curve. In practice this is the system one would want to study, since the parameter values are estimates, and probably won't be precisely on the bifurcation curve.

Remark ([8])
Hypernormal forms (or simplest normal forms) are normal forms where the coefficients of the normal form are chosen such that the initial series becomes finite, as opposed to truncating the series. These normal forms are harder to calculate, and are outside the scope of this thesis.

Starting with the system,

$$\dot{\underline{x}} = \underline{f}(\underline{x}, \underline{\alpha}) \tag{15}$$

experiencing a Hopf-bifurcation at some point $(\underline{x}_c, \underline{\alpha}_c)$, then (see. appendix B) the Jacobian matrix of $\underline{f}$ evaluated at $(\underline{x}_c, \underline{\alpha}_c)$ has a pair of purely imaginary eigenvalues, and

associated eigenvectors $\{\underline{q}, \overline{\underline{q}}\}$ spanning the center eigen space E^c. Since the eigenvalues are known to be non-zero complex conjugate pairs, they are clearly distinct, and the eigenspace E^c is two dimensional.

The process outlined in appendix C assumes the system is transformed to its eigenbasis:

$$\begin{aligned} \dot{\underline{x}}_c &= A^c \underline{x}_c + \underline{f}_1(\underline{x}_c, \underline{x}_s) \\ \dot{\underline{x}}_s &= A^s \underline{x}_s + \underline{f}_2(\underline{x}_c, \underline{x}_s). \end{aligned} \tag{16}$$

By the center manifold theory (app. C), there exists an attractive center manifold given by the graph of some smooth function $\underline{x}_s = h(\underline{x}_c)$. Restricting the system to this manifold, (as opposed to projecting directly to the center eigenspace) has been shown to preserve asymptotic behavior [5]. Orbits close to $\underline{A}_4$ now share asymptotic traits with the first equation in (16) (see app C; attractivity), giving rise to the description of the stable eigenspace as "enslaved" by the center.

It is often convenient to reparameterize the center eigenspace E^c with $(z, \overline{z})$ where, $z \in \mathbb{C}$, that is $\underline{x}_c = z\underline{q} + \overline{z}\overline{\underline{q}}$, where $\underline{q}$ and $\overline{\underline{q}}$ are the eigenvectors of A^c assosiated with the eigenvalues λ and $\overline{\lambda}$ respectively. An explicit expression for the parameter is given by $z = \langle \underline{p}, \underline{x} \rangle$, which can be found in [11].

Remark
The coordinate transformation $\begin{bmatrix} x \\ y \end{bmatrix} \mapsto \begin{bmatrix} z \\ \overline{z} \end{bmatrix}$ *is well defined since it can be expressed by the invertible map:*

$$\begin{bmatrix} z \\ \overline{z} \end{bmatrix} = \begin{bmatrix} 1 & i \\ 1 & -i \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix}$$

Here $\frac{\partial}{\partial z}, \frac{\partial}{\partial \overline{z}}$ *are the Wirtinger differential operators, which (with* $z = x + iy$*) arise naturally as the transformation of* $\frac{\partial}{\partial x}, \frac{\partial}{\partial y}$ *to this new coordinate system. They are given by:*

$$\begin{aligned} \frac{\partial}{\partial z} &= \frac{1}{2}\left(\frac{\partial}{\partial x} - i\frac{\partial}{\partial y}\right) \\ \frac{\partial}{\partial \overline{z}} &= \frac{1}{2}\left(\frac{\partial}{\partial x} + i\frac{\partial}{\partial y}\right) \end{aligned}$$

It is the properties of these derivatives that make $z, \overline{z}$ *appear independent.*

Now the center manifold can be approximated by a power series expansion in the two coordinates $z, \overline{z}$ (see appendix C):

$$\underline{h}(z, \overline{z}) = \underline{b}_{20} z^2 + \underline{b}_{11} z\overline{z} + \underline{b}_{02} \overline{z}^2 + O(|z|^3) \tag{17}$$

Here $\underline{b}_{jk} \in \mathbb{C}^2$ are usually chosen such that $\underline{b}_{jk} = \overline{\underline{b}_{kj}}$ to ensure that $\underline{h}(z, \overline{z})$ be real.

As previously mentioned, on the center manifold (or near the critical point $(\underline{x}_c, \underline{\alpha}_c)$), system (16) is governed by solutions of the equation of $\dot{\underline{x}}_c$. By substituting (17) into the first equation of (16) one gets:

$$\dot{\underline{\xi}} = V(\overline{\xi}) = B\underline{\xi} + f_1(\overline{\xi})) = V^1(\underline{\xi}) + V^2(\overline{\xi}) + V^3(\overline{\xi}) + ...$$

The functions V^i are all the terms in the Taylor expansion homogeneous of degree i. The 2×2 matrix B, representing the linear part of the Taylor expansion in $\underline{\xi}$ (that is $V^1(\overline{\xi}) = B\overline{\xi}$), is similar to A^c. As pointed out in [15], it is now a diagonal matrix with complex entries equal to the eigenvalues of A^c.

In what follows terms in the above equation are removed by a *near-identity* change of coordinate transformation. The general approach for removing the k'th homogeneous function V^k of a Taylor expansion is presented below. It is based heavily on [15]. Other references are [21, 20]. First introducing the coordinate transformation;

$$\tilde{\underline{\xi}} = \underline{\xi} + P^k(\underline{\xi}) \tag{18}$$

with P^k a homogeneous function of degree k considered unknown for the time being. The transformation (18) is close to the identity map in small neighborhoods of the origin, and hence one would expect it to have an inverse. This inverse is given by [15]:

$$\underline{\xi} = \tilde{\underline{\xi}} - P^k(\tilde{\underline{\xi}}) + O(\tilde{\underline{\xi}}^{2k-1}). \tag{19}$$

By substituting this into the original equation one eventually gets:

$$\dot{\tilde{\underline{\xi}}} = V(\tilde{\underline{\xi}}) + \left[DP^k(\tilde{\underline{\xi}})V^1(\tilde{\underline{\xi}}) - D(V^1(\tilde{\underline{\xi}}))P^k(\underline{\xi})\right] + O(|\underline{\xi}|^{k+1}) \tag{20}$$

or alternatively;

$$\dot{\tilde{\underline{\xi}}} = V(\tilde{\underline{\xi}}) + \left[DP^k(\underline{\xi})B\tilde{\underline{\xi}} - BP^k(\underline{\xi})\right] + O(|\underline{\xi}|^{k+1}). \tag{21}$$

In (20) the square bracket is the Lie bracket $[P^k, V^1]$.

If one substitutes $V(\tilde{\underline{\xi}})$ by its Taylor expansion, it is clear that the vector field of $\dot{\tilde{\underline{\xi}}}$ is unchanged up to degrees less than k. The goal is to choose P^k such that it removes the term of order k of the expansion of $V(\tilde{\underline{\xi}})$. To this end the operator $L_B : H^k \to H^k$ is introduced in [15, 20], H^k being the vector space of homogeneous polynomials of degree k. It is given by;

$$L_B P^k = DP^k B - BP^k. \tag{22}$$

showing that it is modeled on the square brackets of equations (20)-(21), and is linear. The condition that it removes the k'th order term can be written as [20],

$$L_B P^k = V^k. \tag{23}$$

This is called the *homological equation* assosiated with the operator B in [20], a term from homological algebra explained well in in [10, p.4-5]. V^k is the terms in the Taylor

expansion of V, homogeneous of degree k. The question now is that of finding an inverse of a linear map from a finite vector space into itself, to determine P^k uniquely. Even in the case when L_B is not invertible, V^k might still be in its range. Note also that there is a freedom in the choice of P^k when $Null(L_B) \neq \{0\}$ since clearly the transformation $\tilde{\xi} = \xi + P^k + \tilde{P}^k$, with $\tilde{P}^k \in Null(L_B)$ is equivalent to $\tilde{\xi} = \xi + P^k$ up to (and including) order k, but is likely to affects higher orders.

Remark
Even if one neglects the arbitrary choice of complement to the the image of L_B in H^k (called the normal form style), the normal form is still not unique. An example of this can be found in [6], for normal forms of the Hopf-bifurcation without the bifurcation parameters.

As is shown in [15], for a Hopf-bifurcation this linear map is given by:

$$L_B P = \begin{bmatrix} \lambda & 0 \\ 0 & \overline{\lambda} \end{bmatrix} \begin{bmatrix} P_z^k \\ P_{\overline{z}}^k \end{bmatrix} - \begin{bmatrix} \frac{\partial P_z}{\partial z} & \frac{\partial P_z}{\partial \overline{z}} \\ \frac{\partial P_{\overline{z}}}{\partial z} & \frac{\partial P_{\overline{z}}}{\partial \overline{z}} \end{bmatrix} \begin{bmatrix} \lambda z \\ \overline{\lambda z} \end{bmatrix} \tag{24}$$

P_z^k and $P_{\overline{z}}^k$ are the component functions of P^k, and $\lambda = \gamma + i\omega$ is the eigenvector of B (and A^c since these are invariant under similarity transformation). The eigenfunctions in the above equation coincide with the natural choice of basis elements for H^k, that is the set of all $\begin{bmatrix} p^k \\ 0 \end{bmatrix}$ and $\begin{bmatrix} 0 \\ p^k \end{bmatrix}$, where p^k are all homogeneous monomials in z and $\overline{z}$ of degree k (that is $z^l \overline{z}^{k-l}$ for a fixed k and $0 \leq l \leq k$). By inserting these back into the equation one can get an expression for the eigenvalues in terms of l and k, and it is shown in [15] that the resonant terms of a general Hopf-bifurcation, which are terms in homogeneous spaces H^j where $Null(L_B) \neq \{0\}$, are those associated with the eigenfunctions $\begin{bmatrix} z|z|^{k-1} \\ 0 \end{bmatrix}$ (when $l = \frac{k+1}{2}$) and $\begin{bmatrix} 0 \\ \overline{z}|z|^{k-1} \end{bmatrix}$ (when $l = \frac{k-1}{2}$) and in both cases only when $k \geq 3$ and k is an odd number.

This finally yields the equation for the normal form of the hopf bifurcation [15]

$$\begin{bmatrix} \dot{z} \\ \dot{\overline{z}} \end{bmatrix} = \begin{bmatrix} \gamma + i\omega & 0 \\ 0 & \gamma - i\omega \end{bmatrix} \begin{bmatrix} z \\ \overline{z} \end{bmatrix} + \sum_{j=1}^{\infty} \begin{bmatrix} a_j z|z|^{2j} \\ \overline{a}_j \overline{z}|z|^{2j} \end{bmatrix} \tag{25}$$

Forgetting about $\dot{\overline{z}}$ since it is completely determined by $\dot{z}$, truncating the series at $z|z|^2$ and labeling $a_2 = l_1$ as the first Lyapunov coefficient, the equation now reads:

$$\dot{z} = (\gamma + i\omega)z + l_1 z|z|^2 \tag{26}$$

This is usually what is refered to as the normal form of the Hopf-bifurcation, and has been shown to be a *topological normal form* (see App. B).

The series (25) is constructed by recursive near-identity change of coordinates, so one could express the entire process of composition of many transformations, by the series $\tilde{\xi} = \xi + P^1 + P^2 + ...$ Embedding the center manifold (17) into the four dimensional space of the original system, one can determine the coefficient vectors $\underline{b}_{jk}$ of (17) such that the center manifold approximation incorporates these recursive coordinate transformations (see Appendix E). Presumably this is what has been done in [1].

2.4 Numerical Simulations

There are obvious issues when using this normal form for a quantitative analysis, rather than qualitative traits like (asymptotic) stability or instability, since by the center manifold theory employed in the preceding section, the normal form approximation approaches the system solutions asymptotically in a neighborhood of the bifurcation point, and hence improves by an increase of time, while the Taylor expansions of the velocity field (6), and power series approximation of the center manifold are both local in nature. This might significantly reduce the region of validity of the normal form approximation.

This section aims to investigate these effects through numerical simulations. The first step would be to construct the analytic continuation of our eigenvalue as found in the normal form above, that is finding $\lambda = \lambda(k_1, k_2)$. The good news is that the characteristic polynomial of the Jacobian matrix of the velocity field (6) is a quartic polynomial, and can be solved symbolically on a computer, so we can create our Taylor series approximation in control-phase space of λ. Unfortunately any attempt to find this closed form of $\lambda(k_1, k_2)$ by means of a symbolic engine, results in memory depletion. The expression is likely too large for practical use, and one is left with the numerical approximations.

However, due to time limitations, an analysis of the normal form in control-phase space will not be conducted here. In stead the parameters k_1 and k_2 are held fixed close to suggested values in [1], that place the equilibrium on the bifurcation curve, and the normal form approximation is studied in phase space. This is unfortunate, since the limit cycle that is created at the bifurcation point, is not visible while $\underline{A}_4$ is on the bifurcation curve.

More precisely, the question is whether the flow $\phi^t_{\underline{\mu}} z_0 \mapsto z_{\underline{\mu}}(t)$ defined by system (26), where $\underline{\mu}$ are the (fixed) parameters, approximates the original system behavior near the bifurcation point, when it is projected to the center eigen space.

The calculations were done using Sage, and following the same procedure as the article [1]. The algorithm for computing the coefficient of the resonant term in the normal form was derived in [11]. Adhering to the notation in [1, 11], the reduced system in question reads;

$$\dot{z} = i\omega z + \frac{G_{21}}{2} z|z|^2. \tag{27}$$

This was found studying the system on the bifurcation curve, where $\lambda = i\omega$ is purely imaginary, so it is in compliance with the normal form (26). The parameter vector

$$\underline{\mu} = [\alpha_1, \beta_1, \mu_1, \phi_1, c_1, k_1, \alpha_2, \beta_2, \mu_2, \phi_2, c_2, k_2]$$

is given by the the values in Table 1, and $k_1 = 0.00331$, $k_2 = 0.00099$. These parameter values where found to place the equilibrium point $\underline{A}_4$ on the bifurcation curve.

The steps of the process are:

1. expand the original systems vector field (6) by a Taylor series. For multivariate vector valued function this has the form:

$$\dot{\underline{x}} = \underline{x}_0 + A\underline{x} + \frac{\underline{B}(\underline{x}, \underline{x})}{2} + \frac{\underline{C}(\underline{x}, \underline{x}, \underline{x})}{6} + O(|\underline{x}|^4)$$

where B and C are symmetric multilinear maps given componentwise by

$$B_i(x,y) = \sum_{j,k=1}^{\infty} \left. \frac{\partial^2 \underline{f}_i(\underline{\xi})}{\partial \xi_j \partial \xi_k} \right|_{\underline{\xi}=0} x_j y_k = \underline{x}^T H^i \underline{y}$$

$$C_i(x,y,z) = \sum_{j,k,l=1}^{\infty} \left. \frac{\partial^3 \underline{f}_i(\underline{\xi})}{\partial \xi_j \partial \xi_k \partial \xi_l} \right|_{\underline{\xi}=0} x_j y_k z_l.$$

H^i is the Hessian matrix of the i'th component function of the vector field $\underline{f}$, given by (6).

2. Introduce the left and right eigenvectors of A, assosiated with the imaginary eigenvalues:

$$A\underline{q} = \lambda \underline{q},\ A^T \underline{p} = \overline{\lambda} \underline{p}$$

and specify vectors completely by $\langle \underline{p}, \underline{q} \rangle = \overline{p}^T q = 1$ and $\langle \underline{q}, \underline{q} \rangle = 1$.

3. Calculate the coefficient G_{21} by the formula derived in [11]:

$$G_{21} = \langle \underline{p}, C(\underline{q}, \underline{q}, \overline{\underline{q}}) + B(\overline{\underline{q}}, (2i\omega_0 I - A)^{-1} B(\underline{q}, \underline{q})) - 2B(\underline{q}, A^{-1} B(\underline{q}, \overline{\underline{q}})) \rangle$$

The eigenvectors $\underline{q}$ and $\underline{p}$ of A where found to be:

$$q = \begin{bmatrix} 0.825726599668 \\ 0.0409585004546 - i0.194369952495 \\ 0.376604900585 - i0.365903682592 \\ -0.0323398297072 - i0.0442231245385 \end{bmatrix}$$

$$p = \begin{bmatrix} 0.115059031566 + i0.0190316935593 \\ 0.0035909076202 + i0.0820028393699 \\ 0.627668624917 - i0.615309266395 \\ -5.20913500013 - i6.57563129065 \end{bmatrix}$$

The eigenvalue λ is given by:

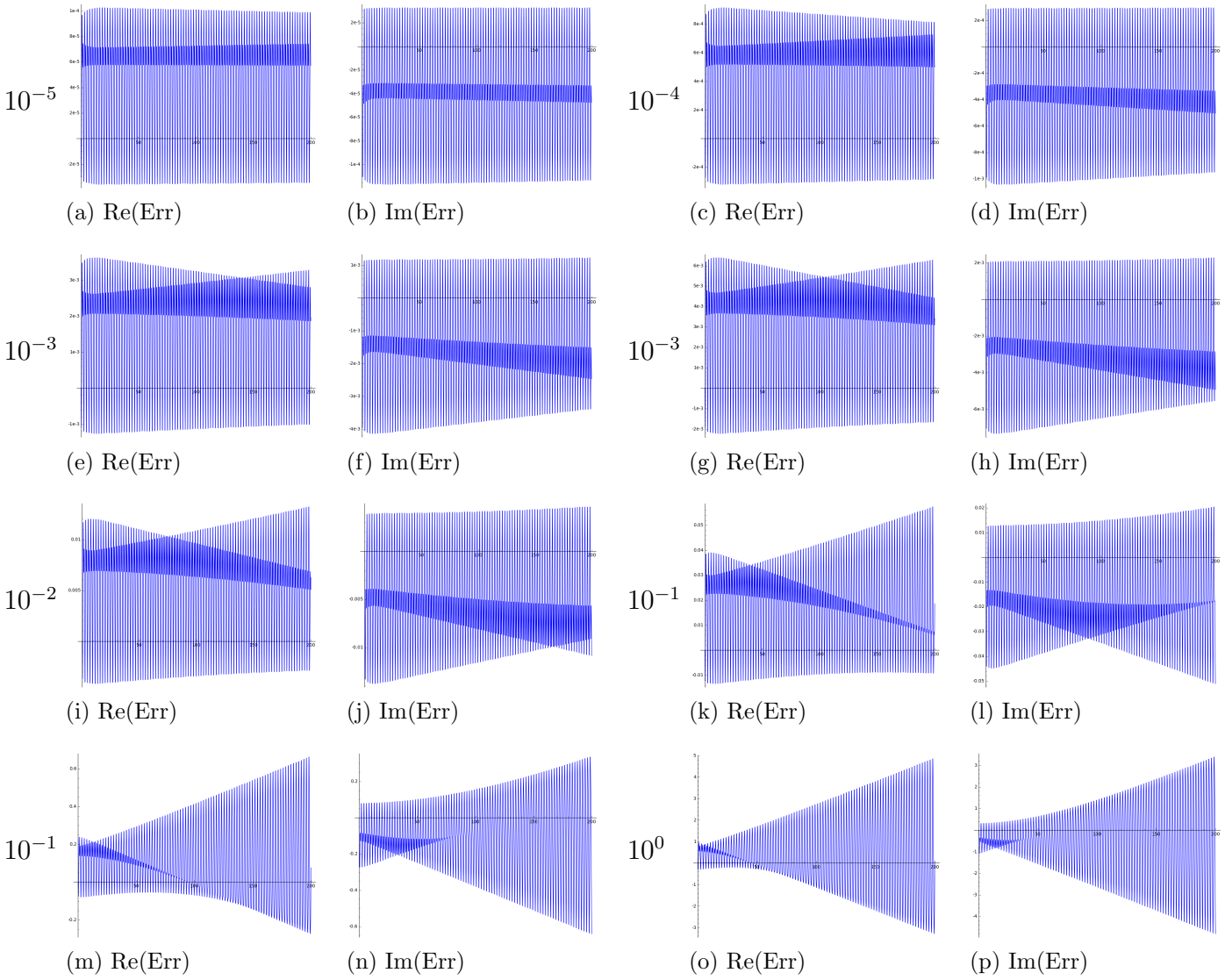
$$\lambda = i\omega = i2.84732034139$$

With these choices of eigenvectors, G_{21} has the value:

$$G_{21} = 1.75924020875e^{-08} + i6.07754066356e^{-08}$$

Now all the coefficients of system (27) have been determined. To get an idea of the phase portrait of the normal form, note that G_{21} is significantly smaller than λ, hence one would expect this to be similar (but topologically distinct from) the system

$$\dot{z} = i\omega z$$



(a) Re(Err) (b) Im(Err) (c) Re(Err) (d) Im(Err)

(e) Re(Err) (f) Im(Err) (g) Re(Err) (h) Im(Err)

(i) Re(Err) (j) Im(Err) (k) Re(Err) (l) Im(Err)

(m) Re(Err) (n) Im(Err) (o) Re(Err) (p) Im(Err)

Figure 1: Figure plotting of Im(Err) and Re(Err) for different initial values for times $t \in [0, 200]$. The initial value deviation from A_4 are given by:

(a)-(b) $(0.1, 0.1, 0.1, 0.1)$

(c)-(d) $(0.3, 0.3, 0.3, 0.3)$

(e)-(f) $(0.6, 0.6, 0.6, 0.6)$

(g)-(h) $(0.8, 0.8, 0.8, 0.8)$

(i)-(j) $(1.1, 1.1, 1.1, 1.1)$

(k)-(l) $(2.0, 2.0, 2.0, 2.0)$

(m)-(n) $(5.0, 5.0, 5.0, 5.0)$

(o)-(p) $(10, 10, 10, 10)$

which can readily be seen to have concentric periodic obits. One would then expect the orbits of (27) to be "almost" closed for most of the phase space. The initial value of the original system ($\underline{IV}_x$), and the normal form (IV_z) are related by:

$$IV_z = \langle \underline{p}, \underline{IV}_x - \underline{A}_4 \rangle \tag{28}$$

Running the numerical simulation on both systems, translating ($\underline{x} - \underline{A}_4$) then projecting ($\langle \underline{p}, \underline{x} \rangle$) the solutions to the original system onto the center eigenspace, we define the error $\underline{Err}$ as the complex vector given by the difference:

$$\underline{Err} = \langle \underline{p}, \underline{x} - \underline{A}_4 \rangle - z \tag{29}$$

Different initial values are plotted in the graphs of Figure 1. The error is cyclic, but does not seem to grow much at first for initial values $k(1,1,1,1)$ where $k \leq 0.8$. From this one can see a sketch of the basin of attraction of the center manifold.

Studying the graphs, one can also see that there is a tendency to worsen, improve, then worsen again as an approximation. This gives some justification to the problems mentioned earlier. At the start of the simulation, the solution of the original system tends exponentially to that of the center system, so the error might be substantial, and accounts for the initial increase. As time goes on, the solutions approach each other and the error is due to the Taylor expansion and center manifold approximation.

Why there is a period in the error is not clear. It could be due to actual displacements, or a difference in the speed traveled between the solutions. Alternatively it could be that the "period" of the cycle is not well approximated by the normal form, and that half a period of the error function represents a 2π phase shift between the two solutions. This, though is not seen when comparing the graphs of the solutions.

Concluding Remarks

The main goal of this thesis, was to show the existence of an invariant set Σ, in the model for biological control presented in [1]. For parameter values proposed in [1], one needs a k_2 of order 10^{-6} for the set to exist. This may not be biologically feasible. There might be other invariant regions of interest in $\mathbb{R}^4$ where volumes contract, that could be less restrictive on the parameter values.

The comparison of the normal form approximation with that of the full system looks promising, but the deviation exhibits a period that has not been accounted for. The simulations are not sufficient to draw any general conclusion on the error array $\underline{Err}$, and could be improved by packing initial values on a hypersphere around the point $\underline{A}_4$. Another natural improvement would be to extend the simulation to control phase space by a numerical continuation of λ near a bifurcation point.

Appendices

Appendix A: Linearization

Most of the theory presented in this section can be found in [3], p. 36-39, with some linear algebra added.

A non-linear system

$$\dot{\underline{x}} = \underline{f}(\underline{x}) \tag{30}$$

can be linearized near a point $\underline{x}_c$ by means of the Jacobian matrix of $\underline{f}$ if it is defined. This is usually the first step when evaluating and classifying fixed points.

By Taylor expanding $\underline{f}$, usually assuming it is C^2 in some neighborhood of $\underline{x}_c$, one gets the the equation

$$\dot{\underline{y}} = \frac{d(\underline{x} - \underline{x}_c)}{dt} = \underline{f}(x(t)) = A_{x_c}\underline{y} + \mathcal{O}(|\underline{y}|^2) \approx A\underline{y}$$

where $\underline{y}(t) = \underline{x}(t) - \underline{x}_c$ is a sufficiently small deviation from x_c to neglect the higher order terms in the expansion, and A is the jacobian matrix of $\underline{f}$ evaluated at $\underline{x}_c$. When $\underline{x} \approx \underline{y}$ the original equation can be restated as a linear approximation near $\underline{x}_c$ as

$$\dot{\underline{y}} = A\underline{y},$$

which has a general solution $\underline{y} = e^{At}\underline{c}$ where $\underline{c}$ is a vector of initial values.

Remark
Solutions to similar matrices of A are determined by the identity $e^{T^{-1}ATt} = T^{-1}e^{At}T$. *Similar matrices have common eigenvalues, and since the eigenvalues determine the type of point, they can be regarded as equivalent. Hence if A is diagonalizable, it can be transformed to D, where the elements of D are the eigenvalues of A*

$$D_{ij} = \begin{cases} 0, & i \neq j \\ \lambda_i, & i = j \end{cases}$$

This greatly simplifies the exponent function:

$$(e^{Dt})_{ij} = \begin{cases} 0, & i \neq j \\ e^{\lambda_i t}, & i = j \end{cases}$$

If A is not diagonalizable, or equivalently, if A is an $n \times n$ matrix, and does not have n linearly independent eigenvectors, there exists an invertible matrix P such that $P^{-1}AP = J$, where J is the Jordan normal form of A. This matrix can be used in much the same way as above, but the diagonal blocks become upper triangular matrices and the components of the solution take the form of:

$$doty_i = y_i^0 e^{\lambda_i t} + y_{i+1}^0 t e^{\lambda_i t} + ... + y_{i+m}^0 \frac{t^{(m-1)}}{(m-1)!} e^{\lambda_i t}. \tag{31}$$

Here m is less than or equal to the size of the diagonal block matrix corresponding to eigenvalue λ_i, and y_i^0 is the i'th component of the initial vector. The thing to note here is that the convergence of this linear combination as $t \to \pm\infty$ is still governed by the value of λ alone since

$$\lim_{x\to\infty} t^m e^{\lambda t} = \begin{cases} 0, & Re(\lambda) < 0 \\ \infty, & Re(\lambda) > 0 \end{cases}$$

So in conclusion, stable (unstable) hyperbolic fixed points, stay stable (unstable) hyperbolic fixed points, after "normalization", even though the matrix is not diagonalizable.

Remark
As a side note, the similarity transformation of the linear map (represented by matrix A) is nothing but a change of basis transformation in both the domain and co-domain of the map. So what is done is representing solutions of (and input to) the linearized system by means of coordinates in the basis of (generalized) eigenvectors of A.

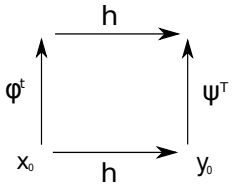


Figure 2: 'Commutative diagram.'

Definition 2.1 (Topological equivalence and conjugacy)
Two systems are topologically equivalent, if there is a homeomorphism h, such that:

$$h \circ \phi^t(x_0) = \psi^T \circ h(x_0)$$

if $t = T$ then the systems are topologically conjugate.

Theorem 2.1 (Hartman-Grobmans Theorem)
Locally, hyerbolic points of a dynamical system
$\frac{d\underline{x}}{dt} = f(\underline{x})$*, where* $\underline{f}(\underline{x_{eq}}) = 0$*, are topologically conjugate to their linearisation*
$\frac{d\underline{y}}{dt} = A\underline{y}$.

This theorem alludes to the dificulties when studying fixed points that are not hyperbolic ($Re(\lambda_i) = 0$ for some i) (See Appendix C on center manifold reduction).

Appendix B; Hopf bifurcation and its normal form

Some terminology is introduced here concerning the classification of bifurcation points. There is only one bifurcation point studied in this paper, which is a Hopf bifurcation. The three other fixed points are hyperbolic (saddle) points, which have a topological conjugate local linearization (by the Hartman-Grobmans theorem).

A *bifurcation* is a change in the topological structure of the systems phase portrait by means of a change in one or more of the systems parameters.

The *codimension* of the bifurcation is usually defined as the smallest number of parameters that need to be changed for the bifurcation to occur. In this thesis, the bifurcation is of codimension-1.

Definition 2.2 (Hopf Bifurcation [3, p.76])
The (non-degenerate) Hopf bifurcation occurs when a dynamical system $\dot{\underline{x}} = \underline{F}(\underline{x}; \underline{\alpha})$*, satisfies the three conditions:*

1. $\underline{F}(\underline{x}_0; \underline{\alpha}_c) = 0$*, where* $\underline{\alpha}_c$ *is the parameter vector at the bifurcation point, and* $\underline{F}$ *is the vector field governing the change of* $\underline{x}$*.*
2. *TheJacobian* $\frac{d\underline{F}}{d\underline{x}}$ *has two purely imaginary eigenvalues, and no other eigenvalues with real part equal to zero.*
3. $\frac{dRe(\lambda)}{d\alpha} \neq 0$ *called the transversality condition.*

It should be stressed that there is no generation or destruction of fixed point solutions near a Hopf bifurcation. This can be seen by looking at the continuation of the vector field $\underline{F}(\underline{x})$ to the extended phase space. Label this continuation by $\tilde{\underline{F}}(\underline{x}, \underline{\alpha})$, where $\underline{\alpha} \in \mathbb{R}^1$ is the parameter vector. Now the map $\tilde{\underline{F}} : \mathbb{R}^{n+1} \mapsto \mathbb{R}^n$ defines a unique curve by the implicit function theorem, traversed by the fixed point as the parameter value varies, since the Jacobian matrix of the vector field $\underline{F}$, never looses full rank during the bifurcation (ie. 0 is not an eigenvalue of the matrix) and hence cannot *branch* out into different curves or disappear. Even in our case where $\underline{\alpha} = \binom{k_1}{k_2} \in \mathbb{R}^2$, the unique curve on the surface defined implicitly by g; $\underline{x}_c = g(k_1, k_2) \equiv \tilde{g}(k_1)$, since $k_2 = k_2(k_1)$.

Definition 2.3 (Normal Form)
The normal form of a bifurcation is a simplification of the system near the bifurcation point, retaining the asymptotic behavior of the full system. For a general Hopf bifurcation, it takes the form [3]

$$\dot{x} = \mu x - \omega y + (\alpha x - \beta y)(x^2 + y^2)$$
$$\dot{y} = \omega x + \mu y + (\beta x + \alpha y)(x^2 + y^2)$$

A topological normal form, is a normal form whose phase portrait is topologically equivalent to the original system in some neighbourhood of the point.

Remark
The normal form employed in this article is [14]

$$\dot{x} = \beta x - y + \sigma x(x^2 + y^2)$$
$$\dot{y} = x + \beta y + \sigma y(x^2 + y^2)$$

which has (with $z = x + iy$) the alternative representation:

$$\dot{z} = (\beta + i)z + \sigma z|z|^2 \tag{32}$$

which scales to:

$$\dot{w} = (\gamma + i\omega)w + l_1 w|w|^2 \tag{33}$$

The value of σ is given by $\sigma = sign(l_1)$. l_1 is the first Lyapunov coefficient, and is used to determine the type of Hopf bifurcation, which can be either sub- or super-critical;

Definition 2.4 (Subcritical / Supercritical Hopf bifurcation [4])
*A **subcritical** Hopf bifurcation is characterized by an unstable limit cycle, about a (asymptotically) stable fixed point. This occurs when the normal form (32) has $\sigma = sign(l_1) < 0$. The limit cycle merges with the fixed point at the bifurcation point and produce an unstable fixed point.*

*A **supercritical** Hopf bifurcation is characterized by a stable limit cycle about an unstable fixed point. This occurs when the normal form (32) has $\sigma = sign(l_1) > 0$. The limit cycle merges with the fixed point at the bifurcation point and produce a (asymptotically) stable fixed point.*

The Hopf bifurcation in this thesis is a supercritical Hopf bifurcation. Some authors (see [11, p.89]) use different definitions of sub- and super-critical Hopf bifurcation, but the above seems to be the clearest.

Appendix C; Center manifold reduction

When dealing with non-hyperbolic fixed points, the system is not guaranteed to be equivalent (homeomorphic) to its linearization in a neighborhood of the point. Here one needs to take into account the non-linear terms of the Taylor expansion.

Looking back at appendix A one sees that even for generalized eigenvectors the systems Taylor expansion can be linearly decoupled:

$$\begin{aligned} \dot{\underline{x}}_c &= A^c \underline{x}_c + f_1(\underline{x}_c, \underline{x}_h) \\ \dot{\underline{x}}_h &= A^h \underline{x}_h + f_2(\underline{x}_c, \underline{x}_h) \qquad\qquad \dot{\underline{x}}_c(0) = \dot{\underline{x}}_h(0) = \underline{0} \end{aligned} \tag{34}$$

since the center eigenvectors are either of distinct eigenvalues, or reside in a purely "non-hyperbolic" Jordan diagonal block. Completely analogous to what is called the *stable manifold theorem*, in which the existence of stable (W^s) and unstable (W^u) invariant manifolds tangent to their respective *eigenspaces* (E^s and E^u) at the fixed point, is proved, there also is a center manifold theorem, which asserts the existence of a center manifold (tangent to the center eigenspace). But first a definition:

Definition 2.5 (local invariance [5])
The local invariant manifold M of system (30) *is a manifold comprised of the set of points S, where,*
$\phi_t S \in S \qquad \forall |t| < T \in R^+$
if $T = \infty$*, then M is called an invariant manifold*

Theorem 2.2 (Center Manifold Theorem [5])
Let $\underline{F} \in C^r$*, with* $\underline{F}(\underline{0}) = \underline{0}$ *and* $r \geq 3$*, then there exists a (locally) invariant manifold M, which can be defined as the graph of some nonlinear map* $\underline{h} \in C^{r-1}(E^c, E^h)$*.*
The center manifold is comprised of the set

$$M = \{(\underline{x}_c, \underline{h}(\underline{x}_c)) | \underline{h}(\underline{0}) = \underline{0}, \frac{d\underline{h}}{d\underline{x}}(\underline{0}) = \underline{0}\}$$

Remark
Two useful properties of the center manifold are:

1. *local invariance of M (with respect to the flow of the system).*
2. *Attractivity ; if* $\underline{x}_h = \underline{x}_s$ *(ie* $E^u = \{0\}$*), then, solutions of system* (34)*, tend exponentially to be governed by the solution to* $\dot{\underline{x}}_c$*.*

More explicitly, the *Atractivity* of the manifold M means that if a solution of $\dot{\underline{x}}_c$ is stable, unstable, or asymptotically stable on the manifold, then the same holds for the original system (30).

By inserting $\underline{H}$ into the original equation, one finds that it must satisfy the equation [5, 3]:

$$D_{\underline{x}_c} \underline{h}(\underline{x}_c)[A^c \underline{x}_c + \underline{f}_1(\underline{x}_c, \underline{h}(\underline{x}_c))] = A^s \underline{h}(\underline{x}_c) + \underline{f}_2(x_c, \underline{h}(\underline{x}_c))$$

or alternativly:

$$N(\underline{h}(x_c)) = D_{\underline{x}_c}\underline{h}(\underline{x}_c)[A^c\underline{x}_c + \underline{f}_1(\underline{x}_c, \underline{h}(\underline{x}_c))] - A^s\underline{h}(\underline{x}_c) - \underline{f}_2(x_c, \underline{h}(\underline{x}_c)) = \underline{0}$$

Solving for h is not always possible, but by the next theorem, it can be approximated to any arbitrary degree of accuracy [5, 7]:

Theorem 2.3
Given any $\underline{\phi}(\underline{x}_c)$ defined on some neighbourhood of $\underline{x}_c = \underline{0}$ such that $\underline{\phi}(\underline{0}) = D\phi(\underline{x}_c) = \underline{0}$.

If $N(\underline{\phi}(\underline{x}_c)) = O(|\underline{x}|^q)$, as $\underline{x}_c \to \underline{0}$ then
$|\underline{h}(\underline{x}_c) - \underline{\phi}(\underline{x}_c)| = O(|\underline{x}_c|^q)$

Usually this amounts to finding a power series and solving for the coefficient (setting the constant, and linear terms of the expansion to zero by the conditions imposed on $\underline{\phi}$).

This entire process is called the *center manifold reduction* method. In the analysis of the Hopf bifurcation, a process outlined in [11] will be employed in the simulations, where (for efficiency) the system is not transformed to its eigenbasis, but uses the Fredholms alternative to decompose a vector into a sum of its hyperbolic and critical/center components. For convenience the process is restated in appendix D.

Appendix D; Projection Method[11]

This method is completely analogous to the center manifold reduction method, but does not require the system to be transformed to its eigenbasis (see appendix A). It does however requires some additional linear algebra:

Introducing the eigenvector $\underline{q}$ and the left eigenvector $\underline{p}$ of the Jacobian matrix of the vector field (30) ($A = \frac{df}{d\underline{x}}$), given by:

$$A\underline{q} = i\omega_0\underline{q} \qquad A\overline{\underline{q}} = -i\omega_0\overline{\underline{q}}$$
$$A^T\underline{p} = -i\omega\underline{p}$$
$$\langle \underline{p}, \underline{q} \rangle = 1$$

with $\underline{p}, \underline{q} \in \mathbb{C}^n$.

Theorem 2.4 (Fredholm Alternative)
For any vector $\underline{y}$ one and only one of these two alternatives hold:

1. $A\underline{x} = \underline{y}$ *(such and $\underline{x}$ exists)*
2. $A^*\underline{z} = 0$, *such that* $\langle \underline{z}, \underline{y} \rangle = 0$ *(such and $\underline{z}$ exists)*

where $A^* = A^T$ for real matrices, and $\langle \cdot, \cdot \rangle$ denotes the usual inner product (ie. $\langle \underline{p}, \underline{q} \rangle = \overline{\underline{p}}^T\underline{q}$).

By the Fredholm alternative theorem it can be shown that by removing the diagonal blocks in the Jordan normal form of the Jacobian matrix A representing the center eigenvectors, the condition that a vector be in the hyperbolic eigen space reads

$$\langle \underline{p}, \underline{x} \rangle = 0, \qquad \forall \underline{p} \in E^c$$

ie. has no components in the center eigenspace. One can now decompose any vector $\underline{x}$ into its hyperbolic and critical/center component:

$$\underline{x} = w\underline{q} + \overline{w}\overline{\underline{q}} + \underline{y}$$

where $w, \overline{w} \in \mathbb{C}$, $\{\underline{q}, \overline{\underline{q}}\}$ spans E^c, and $\underline{y} \in E^h$. These new "coordinates" (w, $\overline{w}$ and $\underline{y}$) are given by:

$$w = \langle \underline{p}, \underline{x} \rangle$$
$$\underline{y} = \underline{y} - \langle \underline{p}, \underline{x} \rangle \underline{q} - \langle \overline{\underline{p}}, \underline{x} \rangle \overline{\underline{q}}$$

Remark
[11] This equation holds since $\langle p, \overline{q} \rangle = \frac{1}{\lambda}\langle p, A\overline{q} \rangle = \frac{1}{\overline{\lambda}}\langle A^T p, \overline{q} \rangle = \frac{\lambda}{\overline{\lambda}}\langle p, \overline{q} \rangle$, when $\lambda \neq \overline{\lambda}$ one gets $\langle \underline{p}, \overline{\underline{q}} \rangle = 0$

From this point on, what is left to do is Taylor expanding the vector field (again using $\langle \underline{p}, \underline{F}(w\underline{q} + \overline{w}\overline{\underline{q}} + \underline{y}) \rangle$ to decompose the result) and finding the center manifold expressed as:

$$\underline{y} = \underline{V}(w, \overline{w}) = \frac{1}{2}\underline{c}_{02}\overline{w}^2 + \underline{c}_{11}w\overline{w} + \frac{1}{2}\underline{c}_{20}w^2 + ...$$

Where $_{ij} \in E^s$ (ie. $\langle \underline{p}, \underline{c}_{ij} \rangle = 0$).

This method is employed when finding the first Lyapunov coefficient [14] given by:

$$l_1 = \frac{1}{2\omega} Re[\langle \underline{p}, \underline{C}(\underline{q}, \underline{q}, \overline{\underline{q}}) \rangle - 2\langle \underline{p}, \underline{B}(\underline{q}, A^{-1}B(\underline{q}, \overline{\underline{q}})) \rangle + \langle \underline{p}, \underline{B}(\overline{\underline{q}}, (2i\omega I_n - A)^{-1}\underline{B}(\underline{q}, \underline{q})) \rangle] \quad (35)$$

Appendix E; Imbedding of the Center manifold

With this method the center manifold is imbedded into the full system dimensions, insted of just the dimension of the hyperbolic eigenspace. For more details consult [12].

Given the system;

$$\dot{\underline{x}} = F(\underline{x}), \qquad F \in C^r(\mathbb{R}^n, \mathbb{R}^n)$$

experiencing a Hopf bifurcation. The (locally) invariant manifold is expressed as a surface in $\mathbb{R}^n$ by:

$$\underline{H}(p_1, p_2) = \underline{v}_c(p_1, p_2) + \sum_{2 \le j+k}^{n} \frac{1}{j!k!}\underline{h}_{ij}p_1^j p_2^k$$

where $\underline{h}_{ij} \in \mathbb{R}^n$ are coefficients to be determined, and (p_1, p_2) parameterize $\underline{x}_c$

Remark

1. *Note that the power series expansion of the two variables lacks constant and linear terms. It has the same form as the usual center manifold approximation.*

   The $\underline{v}_c$ addition accounts for the the movement of critical component of the resulting vector. (formerly this critical component was itself the parameter of the center manifold $\underline{y} = \underline{h}(\underline{x})$)

2. *The vectors $\underline{h}_{ij}$ are sometimes chosen to have no critical component, that is, to be orthogonal to the center eigenspace, but this is not necessary, and this freedom of choice can be exploited to simplify the expression.*

Appendix F; General Theorems and equations

In this appendix some useful theorems are stated.

The flow ϕ^t of system (30) is a map taking $x_0 \mapsto x(t)$ and, by assumption, is continuously differentiable, and traces out integral curves of the vector field f. With limit cycles and fixed points as exceptions, this function is *injective* and one would expect it to have an inverse. This inverse function is given by ϕ^{-t} since, $\phi^{-t}(x) = x_0$. This innocuous observation, shows that it is safe to assume a map between the Euler and Lagrangian flow representation, an observation that will be used in the proof of the next theorem.

The first theorem addressed here, can be viewed as a generalization of the Leibniz rule. Its usefulness is evidenced by the plethora of different formulations in which it is stated. One of which is the following:

Theorem 2.5 (Reynolds Transport Theorem)
Given system (30)*, with velocity field* $\underline{f}$ *and scalar valued function* $\rho(\underline{x}, t)$.
$\frac{d}{dt}\left[\int_{\Omega(t)} \rho d\underline{x}\right] = \int_{\Omega(t)} \frac{\partial \rho}{\partial t} + \nabla \cdot (\rho \underline{f}) d\underline{x}$

Remark
More general statements of the theorem exists, where the boundary is not determined by the flow, and where the function ρ *is vector valued, but these generalizations are not needed in this thesis.*

At the center of the proof is the change of variable theorem from multivariable calculus. The esoteric jargon of continuum mechanics is intentionally left out. A proof can be found in [16].

Note
Since t *is both a variable and parameter, the following notation is adopted:*

$\frac{d\rho}{dt}(\underline{x}(\underline{x}_0, t), t) = \frac{\partial \rho}{\partial t} + \frac{\partial \rho}{\partial \underline{x}} \frac{\partial \underline{x}}{\partial t}$
$D_{\underline{x}_0} \underline{\phi}^t(\underline{x}_0)$ *is the Jacobian matrix of* ϕ^t *at* $\underline{x}_0$

Proof *As was assumed, the flow of system* (30) *given by:* $\underline{\phi}^t(\underline{x}_0) = \underline{x}(t)$ *is invertible, (with inverse* $\underline{\phi}^{-t}(\underline{x}) = \underline{x}_0$ *) hence it has an associated non-zero Jacobi determinant. When evaluating the integral*

$$\frac{d}{dt}\left[\int_{\Omega(t)} \rho(\underline{x}, t) d\underline{x}\right]$$

introducing the change in coordinates, given by the inverse of the flow, results in an integral:

$$\frac{d}{dt}\left[\int_{\Omega_0} \rho(\underline{\phi}^t(\underline{x}_0), t) d\underline{x}\right]$$
$$= \frac{d}{dt}\left[\int_{\Omega_0} \rho(\underline{\phi}^t(\underline{x}_0), t) |det(D_{\underline{x}_0} \underline{\phi}^t)(\underline{x}_0)| d\underline{x}_0\right]$$

The volume of integration is now independent of time (it is compensated for by the integrand) hence it is now possible to move the derivative inside the integral;

$$
\begin{aligned}
&= \int_{\Omega_0} \frac{d}{dt} \left[\rho(\underline{\phi}^t(\underline{x}_0), t) |det(D_{\underline{x}_0} \underline{\phi}^t)(\underline{x}_0)| \right] d\underline{x}_0 \\
&= \int_{\Omega_0} \left[\frac{d\rho}{dt} |det(D_{\underline{x}_0} \underline{\phi}^t)(\underline{x}_0)| + \rho \frac{d}{dt} |det(D_{\underline{x}_0} \underline{\phi}^t)(\underline{x}_0)| \right] d\underline{x}_0
\end{aligned}
$$

Using the Jacobi formula for derivative of a determinant (for invertible matrices) given by:

$$
\frac{d}{dt} det\left(F(t)\right) = det\left(F(t)\right) tr\left(F(t)^{-1} \frac{d}{dt} F(t) \right)
$$

yields;

$$
\begin{aligned}
&\frac{d}{dt} |det(D_{\underline{x}_0} \underline{\phi}^t)| \\
&\qquad = \frac{d}{dt} det(D_{\underline{x}_0} \underline{\phi}^t) \\
&\qquad = det(D_{\underline{x}_0} \underline{\phi}^t) tr\left[\left(D_{\underline{x}_0} \underline{\phi}^t\right)^{-1} \frac{d}{dt} D_{\underline{x}_0} \underline{\phi}^t \right] \\
&\qquad = det(D_{\underline{x}_0} \underline{\phi}^t) tr\left[\left(D_{\underline{x}_0} \underline{\phi}^t\right)^{-1} D_{\underline{x}_0} (\frac{d}{dt} \underline{\phi}^t) \right] \\
&\qquad = det(D_{\underline{x}_0} \underline{\phi}^t) tr\left[\left(D_{\underline{x}_0} \underline{\phi}^t\right)^{-1} D_{\underline{x}_0} (\underline{f}) \right] \\
&\qquad = det(D_{\underline{x}_0} \underline{\phi}^t) tr\left[D_{\underline{x}_0} (\underline{f}) \left(D_{\underline{x}_0} \underline{\phi}^t\right)^{-1} \right] \\
&\qquad = det(D_{\underline{x}_0} \underline{\phi}^t) tr\left[D_{\underline{x}} (\underline{f}) D_{\underline{x}_0} (\underline{\phi}^t) \left(D_{\underline{x}_0} \underline{\phi}^t\right)^{-1} \right] \\
&\qquad = det(D_{\underline{x}_0} \underline{\phi}^t) tr\left[D_{\underline{x}} (\underline{f}) \right]
\end{aligned}
$$

Where $\underline{f}$ is the vector field in (30)*. Absolute value was dropped, since, firstly, at $\underline{\phi}^0(\underline{x}_0)$ $det\left(D_{\underline{x}_0} \underline{\phi}^0\right) = det(I) = 1$ and secondly, here the determinant is continuous, and hence cannot become negative without crossing zero, which breaks with preliminary observations on the flow $\underline{\phi}^t$. The matrix multiplication was interchanged, since it does not alter the value of the trace of the matrix product.*

Now noting that.

$$
tr\left[D_{\underline{x}} (\underline{f}) \right] = \sum_i^n \frac{df_i}{dx_i} = \nabla \cdot \underline{f}
$$

Substituted all this back into the original expression yields:

$$\int_{\Omega_0} \left[\frac{d\rho}{dt} |det(D_{\underline{x}_0} \underline{\phi}^t)(\underline{x_0})| + \rho \frac{d}{dt} |det(D_{\underline{x}_0} \underline{\phi}^t)(\underline{x_0})| \right] d\underline{x}_0$$
$$= \int_{\Omega_0} \left[\frac{d\rho}{dt} + \rho \nabla \cdot \underline{f} \right] |det(D_{\underline{x}_0} \underline{\phi}^t)(\underline{x_0})| d\underline{x}_0$$
$$= \int_{\Omega_t} \left[\frac{d\rho}{dt} + \rho \nabla \cdot \underline{f} \right] d\underline{x}$$

Expanding the derivative of ρ with respect to the "parameter" t gives:

$$= \int_{\Omega_t} \left[\frac{d\rho}{dt} + \rho \nabla \cdot \underline{f} \right] d\underline{x}$$
$$= \int_{\Omega_t} \left[\frac{\partial \rho}{\partial t} + \nabla \rho \cdot \underline{f} + \rho \nabla \cdot \underline{f} \right] d\underline{x}$$
$$= \int_{\Omega_t} \left[\frac{\partial \rho}{\partial t} + \nabla \cdot (\underline{f} \rho) \right] d\underline{x}$$

□

Corollary 2.1
The change in volume element V with respect to time can be written as the integral $\frac{dV}{dt} = \int_{\Omega(t)} \nabla \cdot (\underline{f}) d\underline{x}$

Proof *This follows by setting $\rho(\underline{x}, t) = 1$ in the preceding theorem.* □

The next theorem is stated here for convenience, and will not be proved.

Theorem 2.6
[1] the polynomial $P(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$ with strictly positive real coefficients, satisfying the equation:

$$a_3^2 - a_1 a_2 a_3 > a_1^2 a_4 \tag{36}$$

has a negative real part in all its roots.

Next is a short corollary to the preceding theorem that appears in [1] as an consequence of the theorem. Its validity however, is not obvious to the author, so a proof is presented. It is of importance, since in the article the fact that the Lyapunov coefficient does not change sign is used to disprove a codimension-2 bifurcation on the bifurcation curve (called *generalized Hopf Bifurcation*). This assumes there are no *fold-Hopf bifurcations* (one zero eigenvalue created) or *double-Hopf bifurcations* (a new pair of purely imaginary eigenvalues appears).

Theorem 2.7
The polynomial equation $P(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = 0$ *with real (strictly) positive coefficients has precisely one pair of purely imaginary roots if and only if:*

$$a_3^2 - a_1a_2a_3 = a_1^2a_4 \qquad (*)$$

Proof *First noting that since* $a_4 \neq 0$, $\lambda = 0$ *is not a viable root. Hence roots must come in complex conjugate pairs.*

Assuming the that (*) holds, the equation can be factored as:
$P(\lambda) = \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 = (\lambda^2 - \frac{a_3}{a_1})(\lambda^2 + a_1\lambda + \frac{a_4a_1}{a_3})$

which has precisely one pair of imaginary roots if $\frac{a_3}{a_1} > 0$. *(since* $a_1 \neq 0$*) this proves one direction.*

Now assume $a_3^2 - a_1a_2a_3 \neq a_1^2a_4$ *has at least one pair of imaginary roots, by theorem 2.6 this leaves* $a_3^2 - a_1a_2a_3 < a_1^2a_4$ *as the sole candidate. But if* $P(\lambda)$ *has has root* $\lambda = ib$ *for some* $b > 0$ *it follows that:*

$$\begin{aligned} P(\lambda) &= \lambda^4 + a_1\lambda^3 + a_2\lambda^2 + a_3\lambda + a_4 \\ &= (\lambda^2 - b)(\lambda^2 + a_1\lambda - \frac{a_4}{b}) \\ &= \lambda^4 + a_1\lambda^3 + (-\frac{a_4}{b} - b)\lambda^2 + a_3\lambda + a_4 = 0 \end{aligned}$$

but then

$$a_2 = (-\frac{a_4}{b} - b) < 0$$

contradicting the assumption of positive coefficients. This concludes the proof.□

References

References

[1] Jorge Sotomayor, Luis Fernando Mello, Danilo Braun Santos, Denis de Calvalho Braga, *Hopf bifurcation in a model for biological control*, 2007.

[2] J. D. Murray *Mathematical Biology, Second, corrected edition*, Springer 1993

[3] Ali H. Nayfeh, Balakumar Balachandran. *Applied Nonlinear Dynamics; analytical, computational and experimental methods*. Wiley series in nonlinear science, 1995.

[4] S. Lynch, *Dynamical Systems With Applications Using Matlab*, Birkhauser 2004.

[5] J. Carr, *Applications of center manifold theory* (Applied mathematical sciences, vol. 35) Springer 1981.

[6] P. Yu *Simplest Normal Form of Hopf and Generalized Hopf Bifuractions* International Journal of Bifurcation and Chaos, Vol. 9, No. 10 (1999) 19171939, 1999.

[7] Amartya S. Banerjee, *An Introduction to Center Manifold Theory* Department of Aerospace Engineering and Mechanics, University of Minnesota.

[8] James Murdock *Normal Forms* `http://www.scholarpedia.org/article/Normal_forms`

[9] James Murdock, *hypernormal form theory: Fundations and algorithms*, Journal of Differential Equations - 2004.

[10] James Murdock *Normal Forms and unfoldings for local dynamical systems* Springer, 2002.

[11] Yuri A. Kuznetsov *Elements of Applied Bifurcation Theory* 2. ed. Springer 1998.

[12] Tod K. Leen *A Coordinate independent center manifold reduction*, 1993.

[13] *SageMath, the Sage Mathematics Software System (Version 6.3)*, The Sage Developers, 2014, `http://www.sagemath.org`.

[14] Yuri A. Kuznetsov *Andronov-Hopf bifurcation* Scolarpedia 2006. Visited 29.01.16.

[15] John David Crawford *Introduction to bifurcation theory*, 1991.

[16] J. David Logan - *Applied Mathematics*

[17] `http://www.ipm.ucdavis.edu/PMG/PESTNOTES/pn74137.html`

[18] `http://people.oregonstate.edu/~muirp/biocontr.htm`

[19] Parra, José Roberto Postali. (2014). *Biological Control in Brazil: an overview*. Scientia Agricola, 71(5), 420-429. `https://dx.doi.org/10.1590/0103-9016-2014-0167`

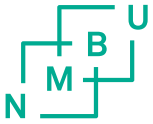
[20] V. I. Arnold *Geometrical methods in the theory of ordinary differential equations*, 1988, Springer

[21] J. Guckenheimer, P. Holmes *Nonlinear oscillations, dynamical systems, and bifurcations of vector fields*, Applied Mathematical Applied mathematical sciences; v. 42, Springer

[22] H. M Yang and S. Ternes, *Estudo dos efeitos de dinâmica vital num modelo de controle biológico de pragas*, Revista de Biomatemática 9, 58-72 (1999).

[23] H. M. Yang, S.Ternes, *Um modelo determinístico para avaliacão do controle biológico de praga de citros* Boletim de Presquisa e Desenvolvimento, Embrapa 3, 1-25 (2002)

[24] S. Ternes, *Modelagem e simulacão da dinâmica populacional da larva-minadora-da-folha-de-citros em interacão com seus inimigos naturais.* Tes de Doutorado, Faculdade de engenharia elétrica e de computacão, unicamp, campinas, Brazil (2001)



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