



Original Research Article

Hopf and torus bifurcations, torus destruction and chaos in population biology



Nico Stollenwerk^{a,*}, Pablo Fuentes Sommer^a, Bob Kooi^b, Luís Mateus^a,
Peyman Ghaffari^a, Maíra Aguiar^a

^aCentro de Matemática, Aplicações Fundamentais e Investigação Operacional, Universidade de Lisboa, Faculty of Science, Campo Grande, Lisboa, Portugal

^bDepartment of Earth and Life Sciences, Vrije Universiteit, Amsterdam, The Netherlands

ARTICLE INFO

Article history:

Received 10 May 2016

Received in revised form 13 December 2016

Accepted 14 December 2016

Available online 3 January 2017

Keywords:

Rosenzweig–MacArthur model

Multi-strain dengue models

Torus bifurcation

Stochastic systems

Stoichiometric formulation

Deterministic chaos

Lyapunov exponents

ABSTRACT

One of the simplest population biological models displaying a Hopf bifurcation is the Rosenzweig–MacArthur model with Holling type II response function as essential ingredient. In seasonally forced versions the fixed point on one side of the Hopf bifurcation becomes a limit cycle and the Hopf limit cycle on the other hand becomes a torus, hence the Hopf bifurcation becomes a torus bifurcation, and via torus destruction by further increasing relevant parameters can follow deterministic chaos. We investigate this route to chaos also in view of stochastic versions, since in real world systems only such stochastic processes would be observed.

However, the Holling type II response function is not directly related to a transition from one to another population class which would allow a stochastic version straight away. Instead, a time scale separation argument leads from a more complex model to the simple 2 dimensional Rosenzweig–MacArthur model, via additional classes of food handling and predators searching for prey. This extended model allows a stochastic generalization with the stochastic version of a Hopf bifurcation, and ultimately also with additional seasonality allowing a torus bifurcation under stochasticity.

Our study shows that the torus destruction into chaos with positive Lyapunov exponents can occur in parameter regions where also the time scale separation and hence stochastic versions of the model are possible. The chaotic motion is observed inside Arnol'd tongues of rational ratio of the forcing frequency and the eigenfrequency of the unforced Hopf limit cycle.

Such torus bifurcations and torus destruction into chaos are also observed in other population biological systems, and were for example found in extended multi-strain epidemiological models on dengue fever. To understand such dynamical scenarios better also under noise the present low dimensional system can serve as a good study case.

© 2016 Elsevier B.V. All rights reserved.

1. Introduction

Ecological and epidemiological systems have many features of non-linear dynamics in common. In relatively complex multi-strain models, describing e.g. dengue fever epidemiology, we have recently come across Hopf bifurcations and further limit cycle bifurcations finally displaying a torus bifurcation and in parameter space soon after also deterministic chaos with positive Lyapunov exponents (Aguiar et al., 2009). Here the torus bifurcation already appears in an autonomous, non-forced system which in this case is nine dimensional.

However, due to the high dimensionality of these models further investigations are quite difficult and especially the question of the influence of noise on the system around the torus bifurcation arises when applying such models to real world data analysis (Aguiar et al., 2011, 2012; Stollenwerk et al., 2012).

Hence a simpler example in population biology could help to understand better the interplay between deterministic bifurcation structure and the population noise. As a prime example, the Rosenzweig–MacArthur model, as a simple only two dimensional model, can serve as such a test bed. It displays a Hopf bifurcation and hence in its seasonally forced version a torus bifurcation. However, the Holling type II response function, which gives the Hopf bifurcation and in forcing the torus bifurcation, cannot be easily used as a population biological model with population noise. It is not directly related to a transition from one to another population class which would allow a stochastic version. Instead, a

* Corresponding author.

E-mail addresses: nico@ptmat.fc.ul.pt (N. Stollenwerk), p.fuentes@outlook.com (P.F. Sommer), bob.kooi@vu.nl (B. Kooi), pgsaid@fc.ul.pt (P. Ghaffari), mafsantos@fc.ul.pt (M. Aguiar).

time scale separation argument leads from a more complex model to the simple 2 dimensional Rosenzweig–MacArthur model, via additional classes of predators searching for prey and predators handling food (see e.g. Metz and Diekmann, 1986, p. 6ff. including a historical account on Holling's original work and its relation to experimental results). Only this extended model allows a stochastic generalization in terms of stoichiometric transitions as a time continuous Markov process, described by a master equation as e.g. frequently used in chemistry and physics, see Stollenwerk and Jansen (2011) and further references in there. We revisited this construction of time scale separation of a larger population model into the Rosenzweig–MacArthur model with Holling type II response function recently in Fuentes Sommer et al. (2015) and in Stollenwerk et al. (2015), and could show good agreement between stochastic higher dimensional version and the reduction to the simple Rosenzweig–MacArthur model around the Hopf bifurcation and the seasonally forced version leading to the torus bifurcation.

Some studies have previously investigated the question of complex dynamics in the seasonally forced Rosenzweig–MacArthur model after a torus bifurcation, primarily (Kuznetsov, 2010) and in more detail (Rinaldi et al., 1993). There in Rinaldi et al. (1993), it was observed that seasonal forcing in different parameters of the model leads to similar bifurcation structures in 2-dimensional bifurcation diagrams with changing seasonality and changing mean value of the forced parameter. The results were obtained by bifurcation analysis via continuation, where fixed points and limit cycles can be followed and Hopf and torus bifurcations can be detected, but no further analysis beyond the torus was possible, especially into the onset of complex dynamics.

Hence here we revisit the analysis of Kuznetsov (2010) and Rinaldi et al. (1993) first with one example of their parameter sets and forcing in the predator birth rate, which gives well the generic pattern observed also in other seasonally forced parameters. But instead of using continuation methods we obtain the information of the bifurcation structure via the complementary method of Lyapunov spectra, here finally also in 2-dimensional parameter space, confirming their rough picture, but now being able to also observe the regions of complex behaviour, namely deterministic chaos, via positive dominant Lyapunov exponents. However, we find the chaotic region close to the torus bifurcation in slightly different regions than speculated by Rinaldi et al. (1993), namely inside Arnol'd tongues. For an introduction to Arnol'd tongues see e.g. Arrowsmith and Place (1990). This is, of course, the explanation why forcing in different parameters give similar results: just the frequency ratio between the forcing frequency and the eigenfrequency of the unforced Hopf limit cycle is of importance for the occurrence of the Arnol'd tongues, not so much which parameter changes the eigenfrequency of the unforced Hopf limit cycle.

Finally, we could leave the parameter regions used in Rinaldi et al. (1993), which do not allow an easy interpretation as stoichiometric system, and found the same qualitative bifurcation structure of Arnol'd tongues in the torus region and their bifurcation into chaos in parameter regions where a time scale separation from a stoichiometric system into the Rosenzweig–MacArthur model is possible, giving now the way to further studies of stochastic processes around the torus bifurcation and the region of torus destruction into chaos.

2. The basic Rosenzweig–MacArthur model

For a prey population X and a predator population Y the Rosenzweig–MacArthur model is in general given in a form similar to the following two dimensional ordinary differential equation

(ODE) system, which was derived e.g. in Fuentes Sommer et al. (2015) from a more extended system, and that can be understood in terms of stoichiometric reactions giving a straight forward stochastic interpretation as used in many population biological systems (Stollenwerk and Jansen, 2011), via time scale separation. It is

$$\begin{aligned}\dot{X} &= \varrho X \left(1 - \frac{X}{\kappa}\right) - k \frac{X}{\tilde{b}N + X} Y \\ \dot{Y} &= -\mu Y + \nu \frac{X}{\tilde{b}N + X} Y\end{aligned}\quad (1)$$

with prey growth rate ϱ and its carrying capacity κ and a predator death rate μ as species specific parameters. Further we have the interaction between the two populations given by a Holling type II response function of the form of $(\tilde{a}X/(\tilde{b} + X)) \cdot Y$ with new parameters \tilde{a} and \tilde{b} , see e.g. Rinaldi et al. (1993). In our case, Eq. (1), the parameters are derived from the more extended system with hunting rate b , handling rate k and predator birth rate ν , with stoichiometric reaction scheme, including a growth limiting resource like space or other food surrogates S as well as food searching predators Y_s and food handling predators Y_h ,



and the relation of prey birth rate β and death rate α giving the growth rate ϱ and the carrying capacity κ by

$$\varrho = \beta - \alpha \quad \text{and} \quad \kappa = N \left(1 - \frac{\alpha}{\beta}\right)\quad (3)$$

used in Eq. (1). For the derivation of Eq. (1) from the extended stoichiometric system (2) see Appendix A and for the stochastic version of this stoichiometric system see Appendix B.

2.1. Parameters used in previous studies

In Rinaldi et al. (1993) the following parameters are given for the Rosenzweig–MacArthur model in the form with Holling type II response function with lumped parameters \tilde{a} and \tilde{b} e.g.

$$\begin{aligned}\dot{X} &= \tilde{r} X \left(1 - \frac{X}{\tilde{\kappa}}\right) - \frac{\tilde{a} X}{\tilde{b} + X} Y \\ \dot{Y} &= -\tilde{d} Y + \tilde{e} \frac{\tilde{a} X}{\tilde{b} + X} Y\end{aligned}\quad (4)$$

with default parameters given in Rinaldi et al. (1993) as $\tilde{\kappa} = \tilde{e} = 1$, $\tilde{r} = \tilde{d} = 2\pi$, $\tilde{a} = 2 \cdot 2\pi$ and $\tilde{b} = 0.3$.

Hence in comparison with our notation we have from these lumped parameters $\varrho = \tilde{r} = 2\pi = 6.283185$, $\kappa = \tilde{\kappa} = 1$, $k = \tilde{a} = 2 \cdot 2\pi = 12.56637$, $b = (\tilde{a}/\tilde{b}) \cdot N = (2 \cdot 2\pi/0.3) \cdot N = 41.8879 \cdot N$, with $N = 1$ by default, $\mu = \tilde{d} = 2\pi$ and $\nu = \tilde{e} \cdot \tilde{a} = 2 \cdot 2\pi$.

2.2. Analysis of the autonomous, unforced system

Now we first analyze the autonomous Rosenzweig–MacArthur model in terms of classical fixed point analysis and its stability analysis and compare with the Lyapunov spectral method, before we then investigate the seasonally forced system.

Download English Version:

<https://daneshyari.com/en/article/5741249>

Download Persian Version:

<https://daneshyari.com/article/5741249>

[Daneshyari.com](https://daneshyari.com)