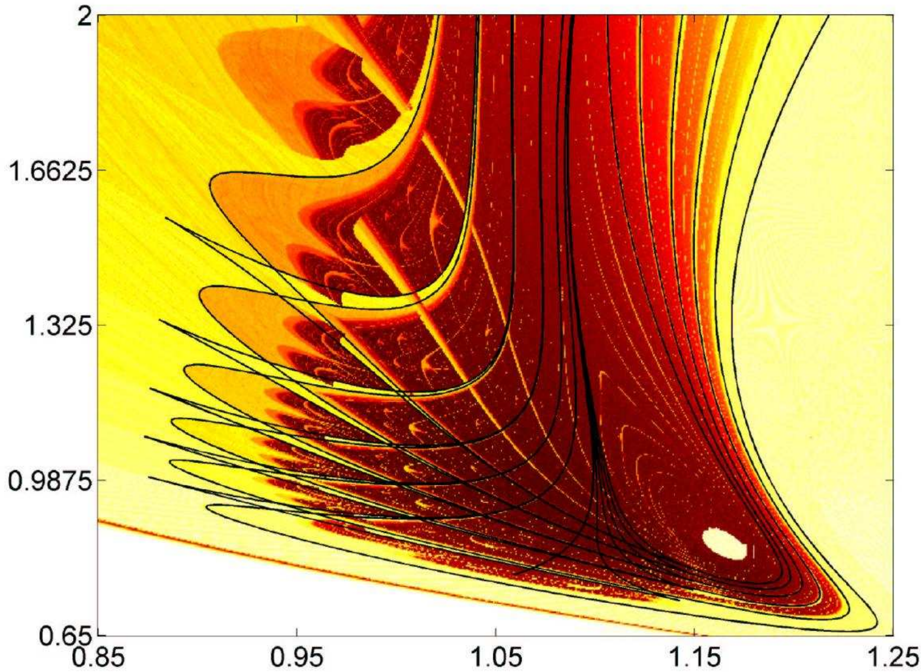
MRI Master Class 2009/2010:
Numerical Bifurcation Analysis of Dynamical Systems
WEEK 15, Apr 13 & 15: Bob Kooi (VU Amsterdam)
Numerical bifurcation analysis of population dynamics



The dynamics of single populations up-to ecosystems, are often described by one or a set of non-linear ordinary differential equations. We will assume that the parameters are all non-negative and that the the right-hand sides depend piecewise-smooth on the state variables: They are continuous but possibly on differential at a finite number of points in the state space. Obviously we are only interested in non-negative solutions. We focus on the application of bifurcation theory to analyse the long-term dynamics of these non-linear dynamical systems. Bifurcation analysis gives regimes in the parameter space with quantitatively different asymptotic dynamic behaviour of the system. This long-term dynamics can be a stable equilibrium, stable periodic solution or chaotic behaviour. Possibly multiple asymptotic behaviours coexist leading to multiple basins of attraction in the state space. A bifurcation analysis gives boundaries in the parameter space of the regions with a specific long-term dynamical behaviour. The changes at the boundaries can be classified as non-catastrophic and catastrophic. Furthermore the bifurcations involved can be local or global. With local bifurcations only knowledge about the (linearized) system in the neighborhood of the equilibrium or limit cycle is sufficient while with global bifurcations connections in the state space are involved. Often environmental conditions are part of the parameter set one is interested in. Important are those boundaries where the biodiversity changes, that is the environmental conditions where species go extinct and other species from adjacent regions can invade. The underlying models for the populations and their interaction can be descriptive such as the classical Lotka-Volterra models or more elaborated models with more biological detail. The latter ones are more difficult to analyse, especially when the number of populations is large. Models of biological processes (feeding, predation, competition) at the individual level are lifted up to the population level and finally ecosystem level whereby besides interactions between populations also interactions with the environment are taken into account. This is easier said than done. Although the procedure is often described as bookkeeping it has been the subject of research for the last 40 years and still a number of deep mathematical open questions.

State variables can be number of individual but also the biomass. Generally the region of interest is assumed to be homogeneous and the total amount is divided by a characteristic size. The resulting quantity is called a density. With no density-dependency the law of mass action gives a product of the two densities as the rate of encounter. The so-called trophic interactions between predator and prey are modelled using the Lotka-Volterra functional response or saturating functions where the amount of prey ingested by the predator saturates when the density of the prey becomes large. Populations van interact with each other in a number of ways but two type are important namely competition and predation. Two types of competition are distinguished: direct or indirect, for instance when both feed on the same food source.

In the literature many models are descriptive. The change in time of each population depends solely on the abundances of the other populations that is the other state variables. Proportionality parameters determine the rate of change whereby superposition is used when a population changes due to multiple mechanisms..

Individual based population models that include age, stage or body size structure are sophisticated, involving partial or functional differential equations, difference equations, or integral equations. For the application of bifurcation theory for these so called physiologically structured population models the reader is refered to the recent paper [1] and references therein.

In this mini-course, we investigate a simple-stage structured model governed by a 2-dimensional system of time-autonomous ordinary differential equations. The equations represent the juvenile and adult stage, respectively. We show that this reduced but biologically-based model predicts, qualitatively, complex population dynamics. Of course, the complexity is restricted by the Poincaré-Bendixson theory. Here we show that multiple equilibria are possible, both stable and unstable periodic orbits can exist and even co-exist, and homoclinic orbits can occur through the interaction of periodic orbits and multiple equilibria.

The best-known two-dimensional ODE system in population biology is the Lotka-Volterra predator/prey model where the dynamic behavior is simple but structurally unstable. In an extension of this model, called the Rosenzweig-MacArthur model, the trophic interaction is described by a hyperbolic functional response instead of a linear functional response. If a carrying capacity for the prey is added, stable oscillations can occur, but no more complex dynamics.

In this mini-course we will give an overview of regular and chaotic dynamics in simple population models (prey-predator, Tri-trophic food chains, etc.) and their bifurcation analysis. Global as well as local bifurcations will be considered. An application in ecotoxicology is also analysed. Bifurcations curves are used with the quantitative assessment of the effects of toxicants on the functioning and structure of ecosystems. The example shows the power of modern numerical techniques for computing these bifurcations to eco(toxico)logists.

In this mini-course we will address three subjects based on the following articles (see the syllabus):

1. Modelling

   - Kooi, B.W. 2003. Numerical bifurcation analysis of population dynamics *Acta Biotheoretica* 51: 189-222.

2. Two-dimensional systems

   - Voorn, v. G.A.K., Hemerik, L., Boer, M.P. & Kooi, B.W. 2007. Heteroclinic orbits indicate overexploitation in predator–prey systems with a strong Allee effect. *Mathematical Biosciences*, 209:451-469.
   - Baer, S.M., Kooi, B.W., Kuznetzov, Yu.A. & Thieme H.R. 2006. Multidimensional bifurcation analysis of a basic two-stage population model. *SIAM Applied Mathematics*, 66(4):1339-1365.

3. Three or more dimensional systems

   - Kooi, B.W., & Boer, M.P. 2003. Chaotic behaviour of a predator-prey system. *Dynamics of Continuous, Discrete and Impulsive Systems, Series B: Applications and Algorithms*, 10:259-272.
   - Doedel, E. J. , Kooi, B. W., Voorn G. A. K. v. and Kuznetzov Y. A. 2008. Continuation of connecting orbits in 3d-ODEs: (I) point-to-cycle connections. *Internat. J. of Bifurcation and Chaos*, 18:1889-1903.
   - Doedel, E. J. , Kooi, B. W., Voorn G. A. K. v. and Kuznetzov Y. A. 2009. Continuation of connecting orbits in 3d-ODEs: (II) cycle-to-cycle connections. *Internat. J. of Bifurcation and Chaos*, 19:159-169.
   - Voorn, G.A.K. van, Kooi B.W. and Boer, M.P. Ecological consequences of global bifurcations in some food chain models, Submitted.

References

[1] O. Diekmann, M. Gyllenberg, J. A. J. Metz, S. Nakaoka, and A. M. De Roos. *Daphnia* revisited: local stability and bifurcation theory for physiologically structured population models explained by way of an example. *Journal of Mathematical Biology*, ??:???–???, 2010.