Numerical bifurcation analysis of ecosystems in a spatially homogeneous environment

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Abstract

The dynamics of single populations upto ecosystems, are often described by one or a set of non-linear ordinary differential equations. In this paper we review the use of bifurcation theory to analyse these non-linear dynamical systems. Bifurcation analysis gives regimes in the parameter space with quantitatively different asymptotic dynamic behaviour of the system. In small-scale systems the underlying models for the populations and their interaction are simple 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. Therefore for large-scale systems the Lotka-Volterra equations are still popular despite the limited realism. Various approaches are discussed in which the different time-scale of ecological and evolutionary biology processes are considered together.

1 INTRODUCTION

In population based models the state of the population is described by one or a finite number of state variables, sucg as the number of individuals, the total biomass and so on. The temporal changes of these variables are mathematically given as one or a set of difference equations (discrete-time) or a set of differential equations (continuous-time). These equations and a rationale together form a model. A phenomenological model is inspired by data. Other models, often called mechanistic, are based on first principles such as conservation laws.

In a food chain each population in consumed by at most one other population. The composition is called a food web when besides this predator-prey interaction other trophic interactions such as omnivory, multiple predators and multiple resources occur. Generally these interactions describe feeding relations among a subset of the species in the community of species living together in a spatially discrete habitat, for example a pond, island and so on. Ecosystems consist of one or more communities which interact with their physical and chemical environment taking into account for instance light supply, energy dissipation, nutrient cycling, immigration, and emigration. Ecosystem ecology is mainly concerned with the functioning of the overall (biotic and abiotic) system.

Nonlinear dynamical system theory was first applied to single population dynamics. May (1976) found that for a population with non-overlapping generations (for instance discrete breeding seasons), described by the logistic discrete time equation (logistic map), a cascade of period doubling ultimately leads to chaotic dynamics when the per capita growth rate is increased. In this paper we focus on the application to continuous time systems. The continuous time version of the logistic equation exhibits only simple dynamics (Gyllenberg et al., 1997).

When descriptive formulations are used for each population the interaction with the environment often remain vague. We will use a mass-balance formulation where the environment has to be specified. This formulation facilitates an integration between population dynamics and the flow of energy, mass and nutrients in ecosystems. We will consider two types of environment, the batch reactor and the chemostat system. The batch reactor is a closed system with no material influxes nor outfluxes. A lake of constant volume where water carrying nutrients flows in at a given rate, and water carrying organisms and nutrients flow out at the same rate (Smith and Waltman, 1994; Morin, 1999) is an example of a chemostat environment.

When the operation conditions are constant the system of ordinary differential equations is called an autonomous system. For these systems it is useful to look for equilibrium states in which the state variables do not change in time. These states, solutions of a nonlinear set of equations, can be stable or unstable. Stable means that after arbitrary small perturbations the system returns asymptotically to this state whereas if unstable it does not. For a specific parameter setting, the stability properties of all equilibria gives knowledge about the dynamics only for initial conditions in the neighbourhood of the equilibria. When an equilibrium is stable it is a point attractor, but there are other types of attractors as well, namely limit cycles, periodic solutions, and chaotic attractors, with sensitive dependency on initial conditions for a given set of parametric values. The set of states from which the solution converges to the attractor is called the basin of attraction. Knowledge of the basins belonging to all attractors yields full information about the dynamic behaviour. Separatrices form the boundary of these basins. Generally they are geometrically smooth but in (Huisman and Weissing, 2002) it is shown by simulation that for models of interaction populations, the basins of attraction may have intermingled fractal geometry. That is, small perturbations in initial conditions can

change the final attractor of the dynamics.

Bifurcation analysis focuses on the dependency of the long-term dynamics behaviour on model parameters (Guckenheimer and Holmes, 1985; Kuznetsov, 1998). In a bifurcation point the asymptotic dynamical behaviour of the system changes quantitatively, for example a stable equilibrium becomes unstable when a parameter is varied. In this way the parameter space is divided into regions with different long-term behaviour. Computer packages are available to calculate the boundaries of regions.

The classical Lotka-Volterra (LV) model (May, 1973) is still popular with modelling large-scale food webs with many state variables and parameters. The main reason for choosing the LV model formulism is that the procedure to calculate the equilibria and their stability and the return time, which is a quantitative measure of the resilience stability in stable equilibria, is straightforward.

For modelling small-scale food webs the linear functional response is often replaced by more realistic population interaction formulations. Many alternative formulations have been proposed. The Holling type II functional response, whereby the consumption rate becomes saturated as the food level increases, is popular. However, with this type of functional response, multiple stationary long-term dynamic behaviours are possible and this complicates the analysis of these models. These models with more biological detail have been analysed frequently using numerical bifurcation analysis. Bazykin (1998) studied various small-scale food web systems. He gives a rather complete overview of the different types of local and global bifurcations.

Throughout this paper we will use (unless stated otherwise) the stability concept derived from mathematics and physics, that is a return to the reference state after a perturbation. We refer to (Grimm and Wissel, 1997) for an inventory and analysis of discussions of ecological stability. They consider 163 definitions of 70 different stability concepts and conclude that: "the general term 'stability' is so ambiguous as to be useless".

In (Stearns and Magwene, 2003) it is stated that: "the ability to study biological processes from a whole genome perspective, is likely to have a profound impact on evolutionary biology and ecology" (see also (Agrawal, 2003)). Here we stress that there are many intermediate steps between genes and ecosystems. First, we have the map from genotypes (DNA sequence) to phenotypes (traits). These traits function as parameters in models that describe the temporal individual behaviour. Individuals can have a complicated life cycle with many life stages, such as: egg, larvae, juvenile and adult, and different modes of reproduction; division and sexual reproduction. Each individual is unique and therefore there is variability at the population level. The "large number assumption" is used to describe the state of a population with a few population state variables and the vital parameters depend anyhow on the parameters of the individual model. Mathematically the population model can be expressed in partial differential equations for a physiologically structured (for instance by age or size) population, delay differential equations for a stage-structured population and a ordinary differential equation for an unstructured population where all individuals are treated identically. In this review only unstructured population models in a spatially homogeneous environment are discussed.

The paper is organised as follows. We distinguish small-scale (few populations) and large-scale (many populations) ecosystem models. We start with small-scale models and demonstrate the bifurcation analysis approach by working out some simple examples. First, we deal with nutrient-population. We calculate the equilibria, perform a stability analysis and study the effects of parameter variation. Thereafter this model is extended by a consumer

population feeding on the resource that consumes the nutrient, (bi-trophic food chain) and thereafter a predator that feeds on the consumer, (tri-trophic food chain). The, mass-balance models for the food chains with different lengths in a chemostat environment are formulated. Comparison with the Rosenzweig-MacArthur (RM) model formulation are made. In both type of models a Holling type II functional response is used to model trophic interactions.

For large-scale ecosystems often the LV model with the linear functional responses is used. Therefore we give a short description of these models and discuss issues such as "Food chain length" and "Complexity and stability of food webs". We relate hypotheses concerning these issues to model predictions. Later on community assembly models are discussed, where we focus on the role of bifurcation analysis. Finally models in which parameters vary on the population and evolutionary time-scale are described.

2 SMALL-SCALE MODELS

One-population models in a closed system

We start with a very simple model for a population feeding on a abiotic nutrient under batch reactor conditions

$$\frac{dN}{dt} = -I\frac{N}{k}\,R \tag{1a}$$

$$\frac{dR}{dt} = \mu\frac{N}{k}\,R \tag{1b}$$

where $N(t)$ is the state of the nutrient mass and $R(t)$ the population biomass. The parameter I is the per capita ingestion rate. The dimension of I is nutrient mass per biomass per unit of time and k nutrient. We assume $\mu = yI$, where y is the efficiency of the nutrient/biomass conversion. In order to obtain mass conservation we introduce products P excreted by the population and defined by the ODE

$$\frac{dP}{dt} = (I-\mu)\frac{N}{k}\,R \tag{1c}$$

Mass conservation gives $d(N+R+P)/dt = 0$. This requires that all state-variables use the same currency, for instance carbon.

Since Equation (1c) is decoupled from Equations (1a) and (1b), we can solve these latter two coupled ODEs first, and thereafter calculate $P(t)$ by substitution of the solutions $N(t)$ and $R(t)$ into Equation (1c).

We can reduce the remaining system of two equations (1a) and (1b) even further. Consider $yN(t) + R(t)$ then $d(yN+R)/dt = 0$. We remark that the state variables $N(t)$ and $R(t)$ do not need to have the same currency here, it is corrected by the dimension of the efficiency. Because the efficiency y is constant the weighted sum of the nutrient mass and population biomass is time-independent. Substitution of $N(t) = k - R(t)/y$ into (1b) yields the single governing equation for the population biomass

$$\frac{dR}{dt} = r(1-\frac{R}{K})\,R \tag{2}$$

where $r = \mu$ and $K = ky$. This is the well-known logistic growth equation where r is the intrinsic growth rate and K the carrying capacity. Observe that this equation is generally

considered to be a descriptive model in which case the exponential growth model, which is the linear term on the right hand side, is augmented with a second order term, the quadratic term, of the Taylor series. Often this term is linked with intraspecific competition for a, not explicitly modelled, nutrient. In another mechanistic interpretation the second term models cannibalism.

The derivation of (2) yields an interpretation of the carrying capacity in terms of (initially) available nutrient $N(0) = k - R(0)/y$ that supports population existence.

Equilibria There is an explicit expression for the solution $R(t)$ for the logistic growth equation (2) but in order to elucidate the bifurcation analysis technique we do not use it here. When interested in the long-term dynamics, we look for stationary solutions where time goes to infinity. Stationary solutions can be equilibria (that is the state variables do not change in time), periodic solutions (that is the state variables change periodically in time) or chaos. The equilibrium equation, where the right-hand side of equation (2) is equal to zero, has two solutions, namely $R^* = 0$ and $R^* = K$. Consequently $R(0) = 0$ implies $R(t) = 0$ for all $t > 0$ and similar when $R(0) = K$ then $R(t) = K$ for all $t > 0$. The next question is whether these equilibria are stable or not.

Notice that although we have one equation there are multiple equilibria. This is typical for nonlinear models where the equilibrium equations are nonlinear as well. In this example the equilibrium values can be calculated easily, but for large ODE systems this can be a tremendous task and they have to be approximated numerically.

Stability Fortunately there is a systematic way to determine whether an equilibrium is stable or not. For that purpose, the system is approximated in the vicinity of the equilibrium point. This approximation yields a linear system, which mathematically is more manageable than a non-linear system. For example, consider the zero equilibrium $R = 0$. When R is small, the second term is small with respect to the first one, $R/K \ll 1$. Therefore $dR/dt \approx rR$ and hence $R(t) \approx R(0)\exp(rt)$. Since the growth rate r is positive, arbitrary small perturbations $R(0) \neq 0$ grow in time exponentially and consequently the zero equilibrium is unstable. In a similar way one can show that the equilibrium $R^* = K$ is stable. That is, after arbitrary small perturbations from $R(0) = K$ the system returns to the equilibrium value, which is the carrying capacity K.

Parameter dependency We continue with the influence of parameter values on the long-term dynamics behaviour. We are interested in those critical values at which the asymptotic behaviour changes qualitatively when the critical values is passed. In the logistic growth example we can take the intrinsic growth rate as a free or bifurcation parameter. Obviously $r = 0$ is a critical point. If $r > 0$ the trivial equilibrium $R^* = 0$ is unstable and at the same time $R^* = K$ is stable. If $r < 0$ (indeed not very realistic from a biological point of view) the trivial equilibrium is stable and the equilibrium $R^* = K$ is unstable. Starting below the carrying capacity, $R(0) < K$, gives convergence to zero, but if starting above the carrying capacity, $R(0) > K$, the population explodes to an unlimited size; the value K is a separatrix.

So, we are looking for parameter values where the stability properties of an equilibrium (or other stationary solution) changes. At this point the system is called structurally unstable. For a one dimensional system with one state variable R, as in the logistic growth case, this is

easy; linearise the right-hand side of the ODE at the equilibrium and set the linear term, the "growth rate", zero. For higher dimensions a similar, but more elaborate, procedure works.

One-population models in an open system

Now suppose that the population lives in an open environment, a chemostat. Then (1) changes into

$$\frac{dN}{dt} = (N_r - N)D - I\frac{N}{k}R \tag{3a}$$

$$\frac{dR}{dt} = (\mu\frac{N}{k} - D)\,R \tag{3b}$$

There are three additional terms which model the interaction with the environment. One for the influx of nutrient, DN_r, two for the outfluxes of the nutrient DN and population DR. The dilution rate D (fraction of the volume replaced per unit of time) and the nutrient density N_r of the inflow medium are the chemostat control parameters that can be experimentally manipulated.

We try to follow the same procedure as for the closed system. Mass conservation is obtained after introduction of a product which leaves the reactor with rate D

$$\frac{dP}{dt} = (I - \mu)\frac{N}{k}R - DP\,. \tag{3c}$$

Mass conservation gives for this open system $d(N + R + P)/dt = -D(N + R + P - N_r)$; not an algebraic equation but an ODE. This equation is the amount of material supplied minus that removed from the reactor, both per volume of the reactor and per unit of time.

We define $H(t) = N(t) + R(t)/y - N_r$ and, since N_r and y are constant, evaluation of the time derivative of H gives directly $dH/dt = -DH$ and therefore $H(t) = H(0)\exp(-Dt)$. Substitution of the solution into (3b) gives

$$\frac{dR}{dt} = \big(\mu\frac{N_r + H(0)\exp(-Dt) - R/y}{k} - D\big)\,R \tag{4}$$

However, this single equation is non-autonomous. Mass conservation gives only a simple algebraic equation at the equilibrium. The original two-dimensional system (3) is asymptotically dynamically equivalent to the one-dimensional system where $H = 0$

$$\frac{dR}{dt} = \big(\mu\frac{N_r - R/y}{k} - D\big)\,R \tag{5}$$

This is the logistic growth equation where $r = \mu N_r/k - D$ and $K = y(N_r - kD/\mu)$ and we discussed its equilibria and their stability in the previous section.

There are two equilibria: the trivial equilibrium $N^* = N_r$ and $R^* = 0$, and the interior equilibrium $N^* = kD/\mu$ and $R^* = y(N_r - kD/\mu)$. The original model is two-dimensional and stability analysis at these equilibria is now more complicated. For a two dimensional system there are two variables, N and R and therefore an equilibrium can be perturbed by varying two variables simultaneously, yielding a much richer repertoire.

Linearization leads now to the following linear set of ODEs. which can be analysed mathematically. There are two resulting exponential growth rates which can be associated with the

so-called eigenvalues of the Jacobian matrix evaluated in the equilibrium. When all eigenvalues are negative it is stable. Unfortunately, this is not a complete picture. There are situations where oscillatory behaviour occurs and the eigenvalues are complex numbers instead of real numbers. Complex numbers have a real part and an imaginary part. When the imaginary part is zero it is in fact a real number. When all eigenvalues have negative real parts the equilibrium is stable, that is, the sign of the eigenvalue with largest real part decides on stability.

The trivial equilibrium $N^* = N_r$ and $R^* = 0$ is stable when $\mu N_r/k - D < 0$ and the interior equilibrium $N^* = kD/\mu$ and $R^* = y(N_r - kD/\mu)$ is stable when $\mu N_r/k - D > 0$. Observe that R^* is non-negative only when the trivial equilibrium is unstable.

In summary: if $\mu N_r/k < D$ then there is one non-negative solution, the trivial solution which is stable. If $\mu N_r/k > D$ then besides the trivial solution, which is unstable, there is one interior solution which is stable. Hence $\mu N_r/k = D$ is a bifurcation curve, called a transcritical bifurcation curve, in the parameter space N_r, D, where all other parameters are fixed. For a given N_r, the population can invade the nutrient system when the trivial solution is unstable, that is when D is not too large. Invasion is possible when the initial rate of increase of the population is positive, that is, its per capita growth rate is larger than its depletion rate. In a biologically context the bifurcation curve marks regions in the parameter space where a population can invade an existing system which was stable before invasion but becomes unstable when the population appears.

When one equilibrium is stable, the other is unstable and vica versa. In general, with multiple equilibria this need not to be true. Therefore we must investigate the stability of all possible equilibria. For biologically relevant problems, we have to investigate only those with non-negative state variables.

One-population model with constant harvesting We used in (3) the Lotka-Volterra or linear functional response based on the law of mass action, where random encounters of individuals of the populations with nutrient particles (molecules or clusters of molecules) in a homogeneous environment are assumed. This means that when nutrient availability increases unboundedly, the ingestion rate of the resource by the population does too. This is not realistic in many practical applications and therefore it is often replaced by a Holling type II functional response in which during a fixed handling period new arriving resource particles are rejected. Then, the ingestion rate is saturating, that is it remains bounded even for abundant nutrient. In order to add realism we introduce an extra per capita loss rate that models for instance biomass loss due to the derivation of energy associated with maintenance needs. These losses can also model other phenomena such as natural death, emigration, harvesting and so on.

Furthermore we introduce a constant loss rate for the population δ_R, for instance due to harvesting. The model then becomes

$$\frac{dN}{dt} = (N_r - N)D - I_{NR}\frac{N}{k_{NR} + N}\,R \tag{6a}$$

$$\frac{dR}{dt} = \left(\mu_{NR}\frac{N}{k_{NR} + N} - D - m_R\right)R - \delta_R \tag{6b}$$

It is possible to find closed-form solutions for the equilibria and the stability conditions for this two-dimensional system. Nevertheless, we present these results graphically in diagrams

where the nutrient supply density N_r and the constant loss rate δ_R are free parameters. We use the species parameter set for bacterium-ciliate models, after (Cunningham and Nisbet, 1983) given in Table 1.

We display the equilibrium biomass R as function of the parameter N_r in Figure 1 for different values of δ_R where $D = 0.02$. For $\delta_R = 0$ essentially the same pattern arises as before. For low nutrient supply the population becomes extinct after inoculation, that is the zero solution is stable. When sufficient nutrient is supplied, right of the transcritical bifurcation TC_1, the population invades into the reactor.

This picture changes drastically for $\delta_R > 0$. For N_r sufficiently high, there are now two positive equilibria. A zero R equilibrium does not exist, even worse when starting with $R = 0$ the solution for the biomass of the population becomes negative. Therefore, after crossing the $R = 0$ axis the model is no longer realistic and we stop simulation. So, it is possible that the population goes extinct in a finite time. In the positive quadrant there is one stable and one unstable equilibrium branch as for $\delta_R = 0$. Now these branches meet in a so called tangent or saddle-node bifurcation T_1 where, similar to the transcritical bifurcation, one eigenvalue is zero. Figure 1 shows the two branches where $\delta_R = 0.001$.

For the case $\delta_R = 0.016$, the biomass in equilibrium R^* is also depicted in Figure 1. At the tangent bifurcation both emanating equilibria are unstable. Increasing N_r now, at a specific value, gives rise to a so called subcritical Hopf bifurcation H_1^+ where the equilibrium becomes stable. The originating stationary periodic solution is an unstable limit cycle. In Figure 2 the unstable limit cycles are shown for different N_r values. Starting inside the limit cycle in the phase plane, the population size converges to the stable equilibrium and starting outside this limit cycle the population becomes extinct. This illustrates that the unstable limit cycle is a separatrix that divides part of the phase space into attracting basins.

Increasing N_r, at a critical point, $G^=$, the limit cycle touches the saddle equilibrium where R is minimum. The (thick) broken cycle is called a homoclinic cycle at this critical parameter value $N_r = 5.667529$. At that point the basin of attraction for the positive stable equilibrium changes; for higher N_r it is the stable manifold of the saddle W_s which is shown partly in Figure 2 for $N_r = 5.75$. So, the critical parameter value where a homoclinic cycle occurs is a bifurcation point whereas the stability properties of all equilibria (the stable spiral sink and the saddle) remain unchanged when the N_r parameter is varied around this point.

A global bifurcation The results in Figure 1 indicate that for $0 < \delta_R < 0.016$, the Hopf bifurcation curve (real parts of the two eigenvalues are zero) emanates from a point on the tangent bifurcation curve (with at least one real eigenvalue zero) and we conclude that both eigenvalues are zero. This codim-two point is called a Bogdanov-Takens point (Kuznetsov, 1998), denoted by BT^+ in Figure 3.

In the same point BT^+ the global bifurcation curve $G^=$ originates. This bifurcation cannot be deduced from local information at the point. One has to integrate the solution whereby starting close to a stationary solution (in our case an equilibrium on the lowest saddle branch); the orbit possibly makes a large excursion through the state space before it comes back to the same stationary solution (homoclinic bifurcation) or lands at another stationary solution (heteroclinic bifurcation). When such a bifurcation occurs the period of the limit cycle tends to infinity. The orbit stays close to the saddle equilibrium for long episodes.

We conclude that in system (6) the minimum value for N_r where a positive equilibrium exists, is for low δ_R values bounded by the tangent bifurcation T_1, but above the BT^+

point bounded by the subcritical Hopf bifurcation H^+. For a fixed δ_R above the BT^+ point the basin of attraction is bounded by the unstable limit cycle and the volume of this basin increases from zero at the Hopf bifurcation. For N_r values above $G^=$ the basin of attraction is determined by the stable manifold of the saddle equilibrium.

These results show that it is not sufficient to study the local stability properties of all equilibria since varying a parameter, global properties can change as well.

Predator-prey models

The resources are now consumed by a consumer of which the biomass is denoted by C. Like for the nutrient–resource interaction, we assume a Holling type II functional response for the consumer–resource interaction. Furthermore, there are per capita loss rates of the living populations. The nutrient–resource–consumer model in the chemostat reads

$$\frac{dN}{dt} = (N_r - N)D - I_{NR}\frac{N}{k_{NR}+N}\,R \tag{7a}$$

$$\frac{dR}{dt} = (\mu_{NR}\frac{N}{k_{NR}+N} - D - m_R)\,R - I_{RC}\frac{R}{k_{RC}+R}\,C \tag{7b}$$

$$\frac{dC}{dt} = (\mu_{RC}\frac{R}{k_{RC}+R} - D - m_C)\,C \tag{7c}$$

Observe that for $C = 0$ the system reduces to the nutrient–resource system discussed in the previous section (except that for the nutrient–resource interaction the LV is replaced by Holling type II functional response). Thus all results obtained for that system are relevant. Again we search for parameter values where the consumer can invade the stable nutrient–resource system which becomes unstable in the nutrient–resource–consumer system which is one dimension higher.

Explicit expressions for all equilibria can be derived straightforwardly. Evaluation of the stability, that is the eigenvalues of the Jacobian matrix evaluated at these points, is much more complicated. Therefore we use a computer program to approximate the bifurcation curves where an eigenvalue or its real part equals zero.

A new version of the Hopf bifurcation the supercritical version is found. For certain parameter combinations the real part of two complex conjugate eigenvalues is zero. At this point the equilibrium, which is first stable, then becomes unstable and eventually a stable limit cycle emanates. This is illustrated in Figure 4. We fix D and vary N_r. For low values the resource cannot invade the reactor with only the nutrient present. On the right-hand side of the transcritical bifurcation TC_1 it can. Increasing N_r further, also the consumer can invade the nutrient–resource system on the right-hand side of TC_2. Unexpectedly, when the system is enriched by increasing N_r, the interior equilibrium becomes unstable and the system starts to cycle at the Hopf bifurcation point denoted by H_2^-. This phenomenon is know as the "paradox of enrichment" (Rosenzweig, 1971).

Reduction is possible with Holling type II functional response when the assimilation efficiency is constant, and $m_R = 0$ and $m_C = 0$. Definition of the function $H(t) = N(t) + R(t)/y_{NR} + C(t)/(y_{NR}y_{RC}) - N_r$ gives $dH/dt = -DH$ and $H \to 0$ for $t \to \infty$.

In the two dimensional RM model the prey population is self-reproducing and its growth

in absence of the predator is modelled using the logistic growth

$$\frac{dR}{dt} = r(1 - \frac{R}{K})R - I_{RC}\frac{R}{k_{RC} + R}\,C \tag{8a}$$

$$\frac{dC}{dt} = (\mu_{RC}\frac{R}{k_{RC} + R} - D - m_C)\,C \tag{8b}$$

To illustrate the relationship between the mass-balance formulation and the RM model we eliminate N with $H = 0$. The resulting term depends on C as well as on R. Consequently, the asymptotic growth rate of the resource depends also on the consumer C whereas with the logistic growth rate it depends solely on R. We conclude that the growth of the resource population is retarded because part of the ingested nutrients are meant for the consumer. The conservation law holds for the whole community and therefore if the resource population itself is consumed this effect is even larger.

If $m_R > 0$ and $m_C > 0$, both the products excreted by the resource population and the consumer population both consist of two terms. One term is associated with the assimilation process which is proportional to the functional response times the biomass and the other is related to the maintenance process and is proportional to the biomass. Observe that the mass-balance model cannot be reduced when $m_R > 0$ and or $m_C > 0$.

Two dimensional autonomous systems and hence also the RM model (8), cannot show chaotic behaviour but three dimensional systems can, (Ott, 1993). The three dimensional mass-balance model (7) is analysed in (Kooi and Boer, 2003) where we found that chaos can occur for biologically meaningful parameter values. Obviously the additional degree of freedom obtained from the modelling of the nutrients explicitly is important.

Small-scale food chain models

If the consumer is in its place consumed by a predator population the food chain consists of three species and one nutrient. The RM model formulation in which the nutrient is again modelled implicitly is studied in the literature to a fair degree. In (Hogeweg and Hesper, 1978) and later in (Hastings and Powell, 1991) it was shown through simulation that chaotic behaviour can occur in the so-called three species (resource, herbivore, carnivore) RM model.

$$\frac{dR}{dt} = r(1 - \frac{R}{K})R - I_{RC}\frac{R}{k_{RC} + R}\,C \tag{9a}$$

$$\frac{dC}{dt} = (\mu_{RC}\frac{R}{k_{RC} + R} - D - m_C)C - I_{CP}\frac{C}{k_{CP} + C}\,P \tag{9b}$$

$$\frac{dP}{dt} = (\mu_{CP}\frac{C}{k_{CP} + C} - D - m_P)\,P \tag{9c}$$

This system has been analysed in great detail by means of bifurcation analyses t(McCann and Yodzis, 1994; McCann and Yodzis, 1995; Kuznetsov and Rinaldi, 1996; Gragnani et al., 1998; Boer et al., 1999; Kuznetsov et al., 2001). The long-term dynamics appear to be very rich. In addition to the familiar local bifurcations, transcritical, tangent (or saddle-node) and Hopf-bifurcation, global bifurcations were found. Sometimes these global bifurcations, such as the saddle-focus Shil'nikov bifurcation (Kuznetsov et al., 2001), form a 'skeleton' for the period doubling of which a cascade leads to chaotic dynamics. In other cases, such as the homoclinic bifurcation for a limit cycle marks interior and boundary crises, see (Grebogi

et al., 1987a; Grebogi et al., 1987b; Ott, 1993; Boer et al., 1999). A discussion of the various types of global bifurcations that are mentioned in the literature on food web dynamics is beyond the scope of this review paper.

In (Letellier and Aziz-Alaoui, 2002; Upadhyay, 2003) the interaction between the consumer and the resource population is modelled by a modified Leslie-Gower scheme described in (Aziz-Alaoui, 2002). The loss in a predator population is proportional to the reciprocal of per capita availability of its most favourite food. The generalist consumer is assumed to reproduce sexually. In this model Equation (9c) is replaced by

$$\frac{dP}{dt} = \mu_{CP} P^2 - I_P \frac{P^2}{k_{CP} + C} \tag{10}$$

Aziz-Alaoui (2002) stated that: "in the absence of the consumer the predator goes extinct if $\mu_{CP} k_{CP} < I_P$ and grows unbounded if the opposite, which is biologically not acceptable". Indeed this trichotomy is similar to that of exponential growth in the case the growth rate is proportional to P instead of proportional to P squared. Nevertheless, if this condition holds similar long-term dynamic behaviour is found, including the crisis route to chaos and the saddle-focus Shil'nikov bifurcation.

If the consumer C is consumed by a predator P then a straightforward extension of system (7) gives

$$\frac{dN}{dt} = (N_r - N)D - I_{NR} \frac{N}{k_{NR} + N} R \tag{11a}$$

$$\frac{dR}{dt} = (\mu_{NR} \frac{N}{k_{NR} + N} - D - m_R) R - I_{RC} \frac{R}{k_{RC} + R} C \tag{11b}$$

$$\frac{dC}{dt} = (\mu_{RC} \frac{R}{k_{RC} + R} - D - m_C) C - I_{CP} \frac{C}{k_{CP} + C} P \tag{11c}$$

$$\frac{dP}{dt} = (\mu_{CP} \frac{C}{k_{CP} + C} - D - m_P) P \tag{11d}$$

Figure 5 gives the stationary biomasses for the tri-trophic food chain as a function of N_r. Again, the results for N_r below the point TC_3, where the predator cannot invade the bi-trophic stable nutrient–resource–consumer system, are the same as those of Figure 4 for the bi-trophic food chain. On the right-hand side of the transcritical bifurcation TC_3 the predator can invade. On the left-hand side of the Hopf bifurcation H_2^- this is via a stable equilibrium of the bi-trophic food chain. However, on the right-hand side of H_2^- the equilibrium of the bi-trophic food chain itself is unstable and there is a stable limit cycle. The invasion criterion is now that the mean rate of increase of the predator size over the limit cycle has to be positive, instead of the rate of increase of the population size at the unstable equilibrium itself. Points in the parameter space where the mean growth rate is zero also mark a transcritical bifurcation, now a transcritical bifurcation of a limit cycle.

The tri-trophic system starts to cycle via a Hopf bifurcation, here denoted H_3^-. This bifurcation for the tri-trophic food chain occurs at a higher N_r value than the Hopf bifurcation H_2^- of the bi-trophic food chain. This means that in the parameter range between these points the predator stabilizes the bi-trophic food chain; it now invades via a stable boundary limit cycle and converges to a stable interior equilibrium.

Biomass distribution under nutrient enrichment Early ecologists like Elton (1927) were able to show that pyramids, by which is meant a decrease in biomass between succes-

sively higher trophic levels, are a consistent feature of real ecosystems (Kondoh, 2003). The calculated biomass distribution for the bi-trophic (Figure 4) and tri-trophic (Figure 5) food chain do not follow this rule. The stable equilibrium biomass distributions are in agreement with the "cascade hypothesis" (van den Berg, 1998). Increases in the nutrient input to the bottom of the system should increase the abundance of the top level and those that are even numbers of levels below the top and not affecting the abundances of those that are odd number of levels below the top. We refer to (Abrams, 1996) for a discussion of the biomass distribution over the trophic levels when the equilibrium is unstable. The tri-trophic results of Figure 5 are often related to the "world is green" proposition (Hairston et al., 1960). The idea is that green plant biomass (the resources) accumulate in the world because predators keep consumers in check (Begon et al., 1996).

Routes to chaos The results in Figure 5 are depicted only for ranges of parameters where the dynamic behaviour is simple, such as an equilibrium or a limit cycle. In a number of papers this mass-balance model of tri-trophic food chain was analysed using numerical bifurcation analysis (Kooi et al., 1998; Kooi et al., 1999; Boer et al., 1998; Boer et al., 2001). A rich repertoire of long-term dynamic behaviour was found for relative high dilution rates and high nutrient supply concentrations. As an example, in Figure 6.a a chaotic attractor in the state-space is shown for the tri-trophic food chain with the per capita loss terms zero.

Chaotic behaviour itself may be interesting, but routes to chaos are also important. The most observed route is via a cascade of period doubling. The system starts to oscillate at a Hopf bifurcation. The emanating stable limit cycle becomes unstable via a so called flip bifurcation. At that point, in addition to the unstable limit cycle, a stable (supercritical version) or unstable (subcritical version) limit cycle with a double period is born. Varying the parameter further, this process repeatedly leads to stable limit cycles with high periods and finally it ends up in chaos. Chaos can also end at boundary crises. Hastings (1996) also discussed this long lasting transient behaviour. This is illustrated in Figure 6 where for an intermediate parameter value a global homoclinic bifurcations to a saddle limit cycle occurs, as pointed out in (Boer et al., 1999). On one side of the global bifurcation point there is coexistence of an interior chaotic attractor and a boundary limit cycle, but on the other side only the boundary limit cycle exist. Here starting in the interior the solution possibly follows the "ghost" of a chaotic attractor for a long time firstly and finally approaches an attractor where the top-predator is absent. Continuation of this global bifurcation in the parameter space for the tri-trophic food chain in the chemostat gives the boundaries of the regimes where chaotic behaviour occurs.

Multiple attractors occur for a considerable variety of control parameter values. Figure 6.a shows two attractors in the state-space. In the chaotic interior attractor all trophic levels coexist and in the other attractor a limit cycle exist in which the top-predator is absent. In general, starting near the saddle equilibrium gives chaotic dynamics whilst if P is initially small the system converges to the stable limit cycle where the top-predator is absent. The boundary between the two regions of attraction (the separatrix) is the stable manifold of a saddle cycle (Boer et al., 1998).

In (Kooi et al., 1999) a top-predator that feeds on the predator is introduced. The bifurcation pattern of this four-species food chain indicate also that regions of persistence for food chains with increasing length are nested. That is, higher nutrient input is required for a top-predator to be able to invade while at the same time the trough-put rate may not be

too high. The interval where invasion is possible is bounded by the transcritical bifurcations $TC_i, i = 1, 2, ...$ The nutrient levels at which these bifurcations occur, increase with the length of the food chain, compare Figure 4 and 5. These equilibria are stable within a nutrient level range between TC_i and H_i^-. This suggests that, theoretically, long food chains can persist.

Small-scale food web models

In food webs different trophic levels are distinguished and a population can consume multiple populations at a lower level. Therefore, at the same time two new trophic interactions can occur besides predator-prey interaction, namely competition for resources where multiple predators consume one resource and one predator consuming multiple resources. In (Kooi and Kooijman, 2000; Kooi and Boer, 2001) we used numerical bifurcation analyses to study the dynamics of a nutrient–resource–competitor–predator system. Competitive exclusion prevents coexistence of the resource and competitor populations feeding both on the nutrient in the chemostat. The equations for this simple food web are

$$\frac{dN}{dt} = (N_r - N)D - I_{NR}\frac{N/k_{NR}}{1 + N/k_{NR}}\,R - I_{NM}\frac{N/k_{NM}}{1 + N/k_{NM}}\,M\ , \tag{12a}$$

$$\frac{dR}{dt} = R\big(\mu_{NR}\frac{N/k_{NR}}{1 + N/k_{NR}} - D - m_R\big) - I_{RC}\frac{R/k_{RC}}{1 + R/k_{RC} + M/k_{MC}}\,C\ , \tag{12b}$$

$$\frac{dM}{dt} = M\big(\mu_{NM}\frac{N/k_{NM}}{1 + N/k_{NM}} - D - m_M\big) - I_{MC}\frac{M/k_{MC}}{1 + R/k_{RC} + M/k_{MC}}\,C\ , \tag{12c}$$

$$\frac{dC}{dt} = C\big(\frac{\mu_{RC}R/k_{RC} + \mu_{MC}M/k_{MC}}{1 + R/k_{RC} + M/k_{MC}} - D - m_C\big)\ . \tag{12d}$$

That is, for the consumer C, both the consumer populations R and the competitor population M are substitutable. This implies that a deficiency in one of the resources can be compensated by using the other, so both are non-essential. Most heterotrophs probably consume resources that are substitutable.

The results for system (12) are presented by one-parameter diagrams where N_r is the bifurcation parameter. The diagram for the nutrient–competitor–predator N, M, C system looks similar to the one for the nutrient–resource–consumer N, R, C system given in Figure 4 except that the system start to oscillate earlier. The reader is referred to (Kooi and Kooijman, 2000) for more detailed results.

For a given dilution rate $D = 0.02$ and without predation the competitor always wins. However, with predation, the results depicted in Figure 7 differ greatly. Below the transcritical bifurcation point TC_{31} the results are those for the N, M, C system. At the point TC_{31} the resource is able to invade this system and the interior solution for the full food web is stable. Increasing N_r this remains true until the transcritical bifurcation point TC_{32} is reached at which the competitor becomes extinct. Hence, above this point the results for the N, R, C system shown in Figure 4 are valid. These results imply the following invasion scenarios. For $N_r = 25$ the N, R, C system can be invaded by the competitor and it replaces the resource population. For $N_r = 50$ the N, R, C system can be invaded by the competitor and the N, M, C system can be invaded by the resource. So, there is mutual invasibility. In both cases after invasion with $N_r = 50$, an interior equilibrium for the whole food web is the result. For $N_r = 75$ the N, M, C system can be invaded by the prey that replaces the competitor. The resulting N, R, C system can not be invaded by the competitor.

When one attractor or multiple interior attractors exist, invasion does not have to lead to convergence to one of these attractors, but replacement can still occur. In (Kooi et al., 2002a; Kuijper et al., 2003) we studied a tri-trophic food web with omnivory, that is the predator consumes the resources as well as the consumer. We showed that crossing a global bifurcation point, invasion of the consumer into the nutrient–resource–predator system leads to convergence to different attractors on both sides of this global bifurcation which is a connection between a boundary equilibrium and an interior limit cycle.

Resources can also be complementary. Then the two (or more) resources are essential at the same time, they cannot be substituted by the other, (Tilman, 1982). Autotrophs require mineral nutrients like carbon, nitrogen, phosphorus and sulfur. These are examples of multiple resources trophic interactions where resources are essential (see Grover (1997)). For essential resources often Liebig's "Law of the Minimum" is assumed where the consumer is limited by only one resource at a time and its growth rate depends on only the abundance of that most limiting resource. The rate of change of the consumer changes discontinuously when another resource becomes most limiting. The final values of the state variables before the switch are their initial values for the dynamics after the switch. Generally the resulting ODE system is well-posed because the Lipschitz condition is satisfied. With respect to parameter changes it is not that simple. The Jacobian matrix evaluated in an equilibrium may change discontinuously with respect to a varying parameter when another resource becomes most limiting. For example limit cycles with positive amplitude can emanate abruptly at a bifurcation point where on the one side of the bifurcation point where the switch occurs, the real parts of all eigenvalues are negative (stable equilibrium) and on the other side they are positive (unstable equilibrium). A formulation without switches and based on mechanistically well-founded principles called a synthesizing unit, is proposed in (Kooijman, 2000).

Ecosystem models

In (DeAngelis, 1992; Gurney and Nisbet, 1998) many examples for small-scale ecosystems are described and analysed. In (Kooi et al., 2002b) the bi-trophic food chain model in the chemostat system (7) was extended with nutrient recycling. Species at both trophic levels digest their food source only partly. The unusable part of the food is ejected in the reactor as faeces together with metabolic products associated with the maintenance process. The excreted material together with dead material, detritus, is decomposed and this gives the recycling of the nutrient. In (Nisbet et al., 1983) it was shown that maintenance has a stabilising effect on predator-prey systems, especially for low dilution rates. The results obtained in (Kooi et al., 2002b) indicate that nutrient recycling counteracts this stabilising effect.

In (Kooijman, 2000) models with much more biological detail about the life history of the individuals that make up the populations, are discussed. With energy and mass fluxes through ecosystems conservation laws are obeyed and stoichiometric contains are taken into account. As an example, in (Kooijman and Nisbet, 2000) the complete mass and energy turnover in a daphnids–algae–bacteria (consumers–producers–decomposers) community in a closed bottle is evaluated. The consumers (daphnids) consume both algae and bacteria. The producers (algae) use solar energy to convert carbon dioxide CO_2 into organic compounds. Bacteria (decomposers) digest their faeces and those of the producers, and dead consumers,

A simplified version of this (consumers–producers–decomposers) community is analysed using numerical bifurcation analysis in (Kooijman et al., 2002). Since decomposition is as-

sumed to be instantaneous the decomposers are not modelled explicitly.

$$\frac{dR}{dt} = \mu_{NR}\frac{M}{K_{NR}+M}\,R - I_{RC}\frac{R}{K_{RC}+R}\,C\;, \tag{13a}$$

$$\frac{dC}{dt} = \big(\frac{1}{r_{RC}} + \frac{1}{r_{MC}} - \frac{1}{r_{RC}+r_{MC}}\big)^{-1} - m_C\big)\,C \tag{13b}$$

$$M(t) = \frac{N}{R(t)} - n_{NC}\frac{C(t)}{R(t)} - n_{NR}\;, \tag{13c}$$

$$r_{RC} = \mu_{RC}\frac{R}{K_{RC}+R} - m_{RC} \quad \text{and} \quad r_{MC} = \mu_{MC}\frac{R}{K_{RC}+R}\,M - m_{MC}\;, \tag{13d}$$

where N is the total amount of nutrient in the biota. The chemical indices n_{NR} and n_{NC} stand for the nutrient content per carbon of the producer and consumer population respectively. The amount of nutrient in the closed environment is taken to be negligibly small; this gives (13c). In the model for the producers (algae) two components (see (Kooijman, 2000) (Kooijman, 2000) , are distinguished, structural biomass R and reserve density (per structural biomass) M. The growth rate of the producers depends on the internal reserve density only, not on the external nutrient availability. The nutritional value of the algae for the daphnids varies. The two components are dynamically independent in spite of the fact that both components are ingested simultaneously according to the Holling type II functional response, see the growth rate terms of r_{RC} and r_{MC}. In (Hanegraaf and Kooi, 2002) both components are assumed to be substitutable but in (Kooijman et al., 2002) they are essential resources for the consumer. This has large consequences for the resulting long-term dynamic behaviour.

When the algae consist of one component, its growth rate of the consumer equals r_{RC}. Then nutrient enrichment gives results very similar to those shown in Figure 4. There are two bifurcations: a transcritical bifurcation and a Hopf bifurcation. With two essential components of the algae, the calculated results are shown in Figure 8. The bifurcation pattern differs substantially from that of Figure 4. The transcritical bifurcation is replaced by a tangent bifurcation T similar to the case $\delta_R > 0$ in Figure 1. In Figure 4 a subcritical Hopf bifurcation H^+ originates, but now in the consumer–producer case, the Hopf bifurcation H^- is supercritical. The emanating cycles from the Hopf bifurcation are stable. Similar to the unstable limit cycles in Figure 1, by increasing the nutrient input level N the stable limit cycle will touch a saddle and becomes a homoclinic loop indicated by $G^=$. For nutrient levels above $G^=$ the solution goes to the stable equilibrium given by $M = C = 0$ and $R = N/n_{NP}$. Hence, when multiple resources are part of a ecosystem its dynamic behaviour depends very much on whether they are essential or non-essential.

3 LARGE-SCALE MODELS

For modelling large food chains and food webs in general the LV model formulation (May, 1973) has been used. The LV model reads

$$\frac{dX_i}{dt} = F_i = X_i\big(-b_i + \sum_{h\in\Delta_i} e_{ih}c_{ih}X_h - \sum_{k\in\Gamma_i} c_{ki}X_k - c_{ii}X_i\big)\;, \quad i = 1\cdots N\;, \tag{14}$$

where N is the number of populations, X_i is the population size, b_i is the intrinsic death rate (or maintenance rate), e_{ih} is the efficiency (yield), c_{ki} is the consumption coefficient and c_{ii}

the intraspecific interaction coefficient which is also called the self-damping or self-regulation intensity. The latter term in (14) models a negative feedback on its own density (sometimes referred to as density-dependent feedback). The set Δ_i is the set of prey species consumed by population i, and Γ_i the predators which consume population i. Comparison with some previous equations shows that the parameter c_{ki} is linked with the maximum ingestion rate used in (1) and c_{ii} with the carrying capacity K occurring in the logistic equation (2). So-called interaction strengths are the entries of the Jacobian community matrix $\alpha_{ij} = \partial F_i/\partial X_j$ evaluated in the equilibrium (positive biomasses assumed)

$$\alpha^*_{ii} = -c_{ii}X^*_i \ , \quad h \in \Delta_i \Rightarrow \alpha^*_{ih} = e_{ih}c_{ih}X^*_i \ , \quad k \in \Gamma_i \Rightarrow \alpha^*_{ki} = -c_{ki}X^*_i \tag{15}$$

The equilibrium equation reads

$$b_i = \sum_{h\in\Delta_i} e_{ih}c_{ih}X^*_h - \sum_{k\in\Gamma_i} c_{ki}X^*_k - c_{ii}X^*_i \ , \quad i = 1\cdots N \ . \tag{16}$$

This is a linear set of non-homogeneous equations for the equilibrium biomasses X^*_i. Information about the local stability is obtained by studying the following linear set of ODEs

$$\frac{dx_i}{dt} = \sum_j \alpha^*_{ij}x_i \ , \quad i = 1\cdots N \ , \tag{17}$$

where $x_i = X_i - X^*_i$ are the disturbances from the equilibrium.

All possible two-dimensional versions can be classified but many questions remain open for higher dimensions (Hofbauer and Sigmund, 1998). Gilpin (1979) was the first to find chaos in a food web consisting of two coexisting prey species and one predator. The dynamics of each population is described by LV equations (14) without intraspecific competition.

In order to reduce the dimension of the governing system in practice often so-called functional groups (Hunt and Wall, 2002) are defined. Species consumed by the same predators and feeding on the same resources are bundled and the vital parameters of these artificial "species" are averages for the group. If each group represents a complete trophic level of a food chain then they are called tropospecies in (Yodzis, 1989; van den Berg, 1998). So, in the state variables of the LV model X_i can be the size, abundance of one species but also that of a functional group or even a complete trophic level.

For ecosystems where the number of functional groups is large, the LV model is popular. The analysis of this model is much simpler than that of the RM-type of models where a Holling type II functional response or its variant for multiple resources, described the trophic interactions. With the linear functional responses the equilibrium equations (16) can be solved easily and only biologically realistic equilibria with non-negative biomasses are a subject of further study. In order to predict the change in the abundance of a population in response to a change in any model parameter, the inverse community matrix approach (Yodzis, 1988; van den Berg, 1998) can be used. The Jacobian matrix has a simple structure and calculation of the eigenvalues is rather straightforward and this gives the stability properties directly.

Large-scale food chain models

For food chains the community matrix is tri-diagonal. The elements on the diagonal represent self-regulation from the intraspecific interaction; the super-diagonal being the prey elements, the negative effects of predator species; the sub-diagonal being the predator elements the

positive effects of prey species. If this system admits an interior equilibrium it is globally stable, this means that all orbits starting with positive biomasses converge to this point, (Hofbauer and Sigmund, 1998).

Food chain length The question of what limits the length of food chains has been problematic ever since Elton (1927) originally asked it decades ago. He observed that food chains usually consist of only three or four links, seldom more. In a previous section we made a remark that long theoretical food chains in an open environment modelled using the mass-balance formalism are possible albeit in a restricted region of the control parameter space with sufficient nutrient input and restricted dilution rate.

The "energetic constraint" hypothesis was suggested by Hutchinson (1959), see also (Pimm and Kitching, 1987). This hypothesis predicts longer food chains in environments with greater energetic input and therefore the observed pattern of just three or four trophic levels could be due to energetic limitations. Experimental results reported in (Pimm and Kitching, 1987) do not support this hypothesis but those reported in (Jenkins et al., 1992) do. Nevertheless, the classical energy explanations for the lengths of food chains has been rejected by a number of ecologists (Begon et al., 1996).

Pimm and Lawton (1977) hypothesised that short food chains are inherently more stable than long ones. In their models, although all communities were mathematically stable, shorter chains had faster return times. Thus longer food chains were dynamically fragile compared to shorter ones. The model used was the LV model with interspecific and intraspecific interactions. Observe that the return time is used as a quantitative measure of the resilience stability in stable webs (see also Grimm and Wissel, 1997).

In (Sterner et al., 1997) the stability of a larger assortment of food web types with a varying number of populations was investigated. They found that stability is strongly related to the fraction of populations with intraspecific interactions. In contrast to the "dynamical constraint" hypothesis, longer food chains were not necessarily less stable.

For food chains upto length four in a chemostat environment the results given in Figures 4, 5 and 7 are partly in agreement with the energetic constraint (nutrient and energetic input is interchangeable). There is a regime where a stable interior equilibrium exists. However, for higher levels of nutrient input this equilibrium becomes unstable, as with the paradox of enrichment, and extinction due to stochastic fluctuations is expected where biomasses are very low. This agrees with the experimental results of Luckinbill (1974). He studied a consumer (*Didinium*)-resource (*Paramecium*) system with a suspension of bacteria consumed by the prey. His result confirmed that due to enrichment dynamics become increasingly unstable and extinction is more likely at higher nutrient levels (Morin, 1999). This aspect of instability of the long food chain was included in the "dynamical stability constraint" hypothesis defined in (Begon et al., 1996).

Large-scale food web models

In food webs generated for theoretical investigations, the interaction strengths of the LV model are assigned randomly (May, 1973). Hence predator and prey roles are assigned at random to two interacting populations without biomass structure in the web, which may allow biologically unrealistic structures (see Chen and Cohen, 2001). Many efforts have been made towards incorporating structural features of natural systems.

In the cascade LV model, Cohen et al. (1990) the trophic structure of the food web model is combined with the population dynamics of the LV model. It assumes a hierarchical relationship between populations that constrains the trophic interaction; hierarchically higher populations are always feeding on populations with a lower trophic level which cannot generate any loops.

In (de Ruiter et al., 1995), a procedure is given for the estimation of the interaction strengths from measured annual average biomasses of all populations, the equilibrium values of the LV model (14). The feeding rates are calculated by assuming that they balance the rates of loss through the (given) natural death the b_i's in (16) and predation. For polyphagous predators the feeding rate per prey is based on the relative biomasses of the prey populations and on the (given) prey preference. The calculation starts with the top-predator of which the loss in only due to the (given) natural death.

Complexity and stability of food webs May (1973) states that randomly introduced complexity destabilizes complex systems. In the generated randomized food webs, biomass structure was not incorporated. In (Neutel et al., 2002) the stability in real food webs is discussed. They show that in real food webs interaction strengths (calculated using the procedure given in (de Ruiter et al., 1995) and described shortly in the previous section) are organized in trophic loops in such a way that long loops contain relatively many weak links. They explain mathematically that this patterning enhances stability. Also the sensitivity of the stability to variation in the values of the interaction strengths is investigated.

Community assembly models

In the ecological community assembly approach starting with resources, newly generated species, (Post and Pimm, 1983), or species from a finite pool of potential colonists, (Drake, 1990), are added one by one at random to an existing food web to form communities. The classical continuous-time LV model (14) was used and the analysis focused on equilibrium behaviour. The main results were that communities become increasingly resistant to invasion, (Post and Pimm, 1983; Drake, 1990), and the possibility of multiple end points; that is, an uninvasible state for a given species pool (Drake, 1990). Their criterion for invasion is completely based on the equilibrium values.

Difficulties are reported in the literature with the simplest application of the community assembly technique (Law and Morton, 1996; Morton et al., 1996; Hastings, 1996; Chen and Cohen, 2001). A stable interior equilibrium may not be an appropriate criterion for community persistence sense it holds possibly only in a arbitrarily small neighbourhood of the equilibrium. Furthermore, even though the equilibrium point is unstable, species can coexist on limit cycles or on more complicated trajectories.

The uninvasible endpoint of the food web assembly is in general not unique. The sequence of food web compositions during the assembly process depends of course on the sequence of species invasions employed.

In this approach species sequentially attempt colonization; between invasions the community approaches a stationary solution. In (Lockwood et al., 1997) species are introduced already when the community is still in a transient state after the last invasion. A simple and fast integrator was used to solve the set of about 60 ODEs. They found that the results depend sensitively on the rate of invasion.

In (Belyea and Lancaster, 1999) environmental constraints are taken into account. For instance dispersal constraints determine the pool of potential colonists available at a particular time. In the paper also disassembly, or the way a community is falling apart, through breakdown of trophic interactions is discussed. Due to hysteretic effects the community does not disassemble in the reverse order in which they were added by invasion. In (Scheffer et al., 2001) catastrophic shifts in ecosystems are explained by existence of alternative stable equilibria between two tangent bifurcations. If the nutrient level is varied a hysteresis loop occurs. In shallow lakes a loss of transparency and vegetation occurred due to human-induced eutrophication. A temporary strong reduction of fish biomass was used as a 'shock therapy' to bring the lakes back to a permanent clear state.

Both the ecological time-scale and the evolutionary time scale biological processes are considered within the same framework in (Drossel et al., 2001). Here new species are added due to speciation events, whilst species become extinct due to coevolution and competition. In the food web model the trophic interactions are modelled using the ratio-dependent functional response (Arditi and Ginzburg, 1989). The model they use is stochastic since the traits and the speciation events are chosen randomly. At a speciation event a new population consisting of one individual that differs from parent chosen at random by one randomly chosen feature. The population dynamics simulation is continued until all surviving species reach an equilibrium. In this way they introduced a separation of the two time-scales.

When the attractor is close to a bifurcation point the asymptotic behaviour within a evolutionary time-step can be very slow. In that case, bifurcation analysis can give additional information. Only the bifurcation pattern close to the attractor has to be studied. When chaos is detected, the bifurcation diagram has to be studied, especially the occurrence of global bifurcations in the region of interest, see also (Hastings, 1996).

4 VARIABLE PARAMETER MODELS

In variable parameter population models some parameters vary when the population's environment changes. In behavioural ecology models variation occurs when the food source composition or the predation pressure changes. These changes can occur on a short-term time scale in which case one can think of prey preferences, inducible defences, and on a long-term time scale in an evolutionary sense where changes occur due to mutations.

Behavioral ecology models

In (Abrams, 1999) mathematical models are used to investigate the consequences of non-instantaneous choice of a predator population between two prey types. It is a one-consumer–two-resources extension of the RM bi-trophic food chain model (8). The growth of the two self-reproducing resources are modelled by a logistic growth. The model for the interaction of the consumer with the two resources resembles that of the mass-balance model (12) except for the consumption rate that varies in time. There is a trade-off between the consumer consumption rate of the two resources I_{RC}/k_{RC} and I_{MC}/k_{MC} such that the sum of these two consumption rates remains constant. The adaptive adjustment of the consumption rates is at a rate proportional to the change in consumer fitness per unit change in consumption rates. This dynamic is derived from quantitative genetic and phenomenological behavioural models. In (Matsuda et al., 1996) a similar formulation is used for consumer population traits

influencing their choice between alternative resource populations and the resource populations defence traits.

The effects of the specificity of antipredator behaviour (defence) on biodiversity and community complexity is studied in (Matsuda et al., 1996). They assume that all predator species change in their prey choice and all prey species have evolutionary change in their defence effort in evolution. The traits of each species change in an adaptive manner. The rate of this change is proportional to the slope of their fitness function.

Resource populations with inducible defence occur in a wide range of ecosystems. Such inducible defences include refuge use, reduced activity, production of toxins and formation of colonies, helmets or spines. A food chain consisting of algae (resource), herbivorous rotifers (consumer) and carnivorous rotifers (predator) has been studied in (Vos et al., 2003). Algae differ in edibility to rotifers, owing to inducible colony formation and rotifers vary in edibility to consumers rotifers, to inducible spine formation or size differences. Colonies and spines effectively lower the maximum ingestion rates achieved by gape-limited consumers.

In (Vos et al., 2003) inducible defended species are divided into an undefended and a defended subpopulation with different but given parameter values for the maximum ingestion rates. When the predation pressure changes, a transfer between the subpopulations occurs without affecting the total size of the population. Bifurcation analysis of the resulting system (extensions of the RM model (8) and (9)) revealed that inducible defence has a stabilizing effect for the bi-trophic algae rotifer system. For the tri-trophic system parameter values were found where nutrient enrichment does not lead to oscillatory behaviour (as is the case of the tri-trophic food chain of which results are given in Figure 5); the equilibrium remains stable upto very high nutrient levels.

Now we discuss a model based on the LV formulation which is also applied to large-scale models. In (Kondoh, 2003) it is shown that short-term selection on trophic links, arising from a consumer's adaptive food choice is a key to the long-term stability of complex communities. Here an index for food web stability is the probability that all species persist for a given time in fluctuating environment, which was called: "persistence through time of an ecological system" in (Grimm and Wissel, 1997). The consumption coefficient of prey h consumed by predator i, c_{ih} in (14) is written as a product of two factors $c_{ih} = f_{ih}a_{ih}$; f_{ih} is called the foraging efficiency and a_{ih} the foraging effort. If $h \notin \Delta_i$ then $a_{ih} = 0$ and $\sum_{h\in\Delta_i} a_{ih} = 1$. The dynamics of the foraging effort of an adaptive predator i to prey j is given by (Matsuda et al., 1996; Abrams, 1999)

$$\frac{da_{ij}}{dt} = G_i a_{ij}\big(e_{ij}f_{ij}X_j - \sum_{h\in\Delta_h} a_{ih}e_{ih}f_{ih}X_h\big)\ , \quad i = 1\cdots N\ , \tag{18}$$

where G_i is the adaptive rate of consumer i. Hence, this approach includes both population (G_i of the same other as the population growth rate) and evolutionary dynamics (G_i much smaller than the population growth rate) of a system and includes multiple prey species and multiple predator species.

Adaptive models

Adaptive dynamics (Metz et al., 1996; Marrow et al., 1996; Dieckmann and Law, 1996; Geritz et al., 1997; Geritz et al., 1998) is based on a separation between the population dynamical and mutational time scales. Evolution proceeds by the continual replacement of resident types by novel mutants, where feedbacks via the environment are taken into account.

The relationship between adaptive dynamics and optimization models and matrix games is given in (Meszéna et al., 2001). With optimization models a fitness is directly attached to each trait. Traits with higher fitness out-compete traits with lower fitness, so the trait with the highest fitness takes over the population. The matrix game descends from game theory. The evolution of the traits are described by the so called replicator dynamics (Hofbauer and Sigmund, 1998) similar to equation (18). The canonical equation of adaptive dynamics describes the trait substitution sequence in the trait space (Dieckmann and Law, 1996). Evolutionary singular traits are the stationary points of these adaptive dynamics. Explicite rules containing the first and second order derivatives of the fitness with respect to the trait of the resident and the mutant determined the stability (now in trait space) of these singular traits (Geritz et al., 1998). We refer to (Meszéna et al., 2001) for further details.

In (Diekmann, 2002) the following example is given. In the chemostat, besides the nutrient, two populations are present, the resident R populations and the mutant population M. In addition to the interaction between the two populations there is also interaction with the environment (the common resource in the chemostat). The dynamics of the two populations is described by equations (12a), (12b) and (12c) in absence of the predator, $C = 0$. The yield coefficient is considered as trait, so the resident has trait $y_{NR} = \mu_{NR}/I_{NR}$. The mutant population M has trait $y_{NM} = \mu_{NM}/I_{NM}$ and all other parameters are the same as those of the resident. Whether a mutant population can invade depends on the invasion exponent

$$y_{NM} I_{NM} \frac{N^*/k_{NM}}{1 + N^*/k_{NM}} - D - m_M \ . \tag{19}$$

where N^* is the equilibrium value where $M^* = 0$ and R^* follows directly from (12a). Sometimes this expression is called invasion fitness (Metz et al., 1992), that is, their capacity to increase in numbers. This fitness depends on the environment via N^* which is set by the resident population. If this exponent is positive, the mutant can invade, that is, the virgin equilibrium is unstable when the dynamics of the mutant is taken into account. In this example, the mutant will replace the resident (the value of R^* is unimportant in this case!). However, when a predator is present this will depend on environmental conditions. Observe that the requirement of the invasion exponent to be zero also determines a transcritical bifurcation point where the yield $y_{N,M}$ is the bifurcation parameter.

The invasion generates a trait substitution and subsequently mutation and natural selection can lead to a trait substitution sequence. However, the yield has a maximum when all the ingested nutrient is converted into population biomass. In nature increase of the yield comes with physiological costs. Taking that into account leads to a yield $0 < y < 1$, the endpoint (singular trait) of the trait substitution sequence, see again (Diekmann, 2002) for the details.

In this approach transient population dynamics remains completely out of sight. It is assumed that the interior attractor is unique and global attracting. The invasion fitness depends only on the biomasses of the populations and their surroundings. Bifurcation analysis can be applied to find regimes in the parameter space where the requirement that the interior attractor is unique and global attracting is satisfied. The procedure to find conditions for invasibility is essentially the same as the one applied in numerical bifurcation analysis.

Observe the resemblance of this procedure to the community assembly approach. Here mutants try to invade an attractor which becomes unstable by taking the invader into account even when its biomass is zero. However, in adaptive dynamics the invader population differs slightly from the resident population and therefore the new attractor is close to the previous

one. However this needs not always to be the case, see Geritz et al. (2002). They study evolution with multiple attractors in the trait state space. A catastrophic bifurcation, for instance homoclinic and heteroclinic orbits, bring forward phenomena like evolutionary suicide where both the resident and the mutant become extinct.

A similar phenomenon is described in (Bazykin, 1998). He studied a predator-prey system where the prey model allows for an Allee effect. When the predator increases its growth rate beyond the heteroclinic orbit critical value, both populations become extinct.

5 DISCUSSION

Recently in (Fussmann et al., 2000; Shertzer et al., 2002), predator prey cycles in an aquatic community consisting of a mineral resource (nitrogen), producer (green algae) and herbivore (rotifer) where found both experimentally and theoretically. The model is essentially the mass-balance model (7) where the consumer population is described by two state variables, the total rotifer biomass B and the biomass of the reproducing fraction C

$$\frac{dC}{dt} = \left(\mu_{RC}\frac{R}{k_{RC}+R} - D - m_C - \lambda\right) C \tag{20a}$$

$$\frac{dB}{dt} = \mu_{RC}\frac{R}{k_{RC}+R}\, R - (D + m_C)\, B \tag{20b}$$

The parameter λ is the decay rate of fecundity and m_C the mortality rate of the herbivore. This model shows, for the parameter range chosen in (Fussmann et al., 2000), coexistence at equilibrium, coexistence on limit cycles, or extinction of the predator or both populations. Qualitatively similar results were obtained with model (7) of which the results are depicted in Figure 4. It was concluded that the qualitative dynamical behaviour of this system consisting of equilibria, cycles and extinction is highly predictable by the simple model (7) where (7c) is replaced by (20).

Concrete evidence of chaotic dynamics in real populations has rarely been found. Causes are environmental stochasticity, biological variablity, poor data quality, but also the simplifying assumptions made to keep models manageable.

Studying the dynamics of the community can be performed by simulation at given initial values. Gaining insight into the dynamic behaviour of the community under various environmental conditions with this method will be computer-time consuming and large amounts of data will be generated. Finding the desired information from this bulk of data can be a formidable task.

An equilibrium of a dynamic system is just the solution of a set of algebraic equations, the equilibrium equations in which the changes of all state variables are set to zero. If the dimension of the system is high with multiple solutions, then it can still be problematic to find all the solutions. If multiple attractors (equilibria, limit cycles) exist, the state space is divided into different regions, the basins of attraction of which each attractor has one. Starting in a particular point in a basin, convergences to the specific attractor to which the basin belongs. Finding the boundaries of these basins gives in a compact fashion a good overview of the long-term dynamics depend on initial conditions. In general the boundaries have a lower dimension than the total state space and therefore calculation of the basin boundaries saves computing time. Sometimes, performing simulations in time and starting in a sufficiently dense grid in the region of interest in the state space, is the only way to go; for instance if the basins of attraction are fractal.

If sensitivity of the long-term dynamics with respect to parameters is the subject of interest, we can repeat the calculations for different parameter settings and study the enormous amounts of data gathered in this way. In the case that the sensitivity with respect to the initial state variable is smooth, a reduction of efforts can be obtained by dividing the parameter space in regions with a specific long-term dynamic behaviour, such as stationary or oscillatory, or the composition of the community at the final state. It is advantageous to look for the boundaries of these regions, now in the parameter space. This presupposes that there is a criterion which can be checked to determine which region applies for specific parameter values. This is precisely what bifurcation analysis does. Coupled with continuation techniques it gives the opportunity to divide the parameter space in regimes with qualitatively different long-term dynamic behaviour. In the biological sense, it gives the circumstances under which a community can survive or, for example, how much fish can be landed without the danger of extinction.

In this review we have explained the bifurcation analysis approach by elaboration of some case-studies. The results are obtained as simple expressions derived by 'pen and paper' or computer packages such as Maple and Mathematica to perform symbolic operations. In practice this is seldom the case and one has to use computer packages, we mention: AUTO (Doedel et al., 1997), LOCBIF (Khibnik et al., 1993), CONTENT (Kuznetsov and Levitin, 1997), DsTool (Back et al., 1992) and XPPAUT (Ermentrout, 2002).

A complete description of all possible uninvasible endpoints of a community assembly is problematic. In practice, using intermediate results, the parameters associated with the numerical algorithms (tolerances, continuation step size and discretization constants) have to be adjusted interactively by the user, so it seems impossible to generate complete bifurcation diagrams in a stand-alone process. It is a challenge to apply the bifurcation analysis approach, based on nonlinear dynamics system theory, to large-scale food webs and variable parameter models. That the bifurcations pattern, which include both local and global bifurcations, are robust with respect to model formulations is promising. This insight obtained from small-scale food webs can be used to find the relationship between web structure and dynamics in large-scale food webs.

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Table 1: Parameter set for bacterium-ciliate model, after (Cunningham and Nisbet, 1983). The control parameters that can be experimentally manipulated are D and N_r.

Parameter	Unit	Values				
		$i = N$		$j = C$		$j = P$
		$j = R$	$j = M$	$i = R$	$i = M$	$i = C$
$\mu_{i,j}$	h^{-1}	0.5	0.42	0.2	0.3	0.15
$I_{i,j}$	h^{-1}	1.25	1.25	0.333	0.333	0.25
$k_{i,j}$	$\mathrm{mg\,dm}^{-3}$	8.0	5.5	9.0	9.1	10.0
m_j	h^{-1}	0.025	0.025	0.01		0.0075

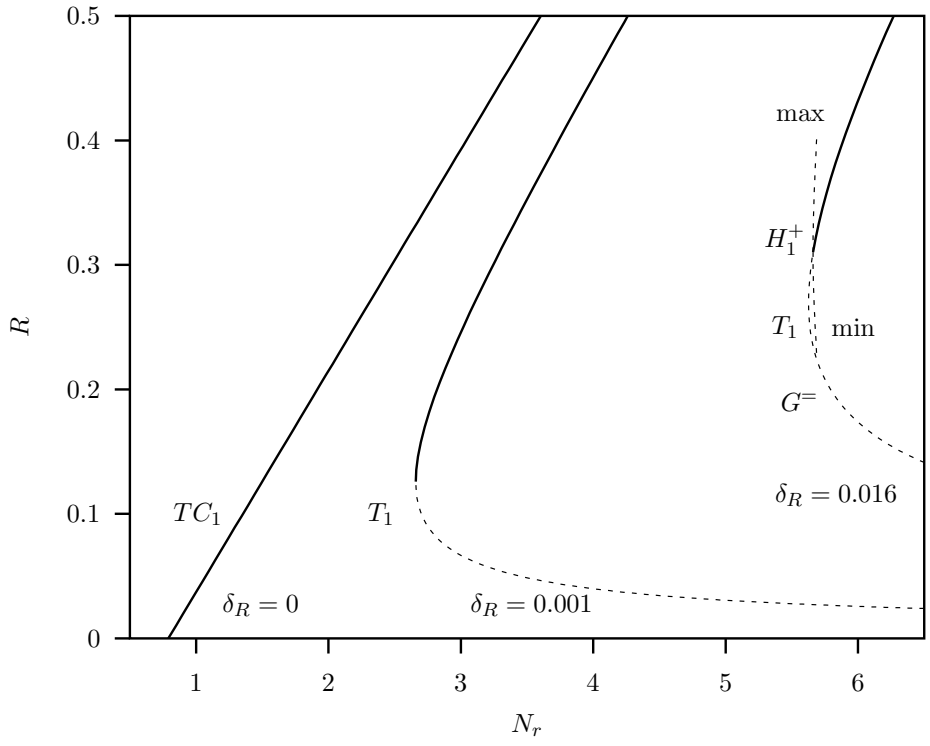

Figure 1: A one-parameter bifurcation diagram for a population (6) in the chemostat. The equilibrium biomass of the resource R is depicted as function of the nutrient level N_r for three parameter values of the harvesting rate δ_R. For $\delta_R = 0$ there is a transcritical bifurcation TC_1.below which the resource population is washed out. For $\delta_R = 0.001$ there are two equilibria on the right-hand side of the tangent bifurcation T_1. One is stable and the other unstable. The stable manifold of the unstable equilibrium acts as separatrix, the boundary of the basin of attraction of the stable equilibrium. Below the tangent bifurcation the resource population goes extinct. For $\delta_R = 0.016$ the stable branch becomes unstable via a subcritical Hopf bifurcation H_1^+. The emanating cycle of which the extrema are also depicted are unstable and form the boundary of the basin of attractions for the stable equilibrium. Below the Hopf bifurcation the resource population goes extinct.

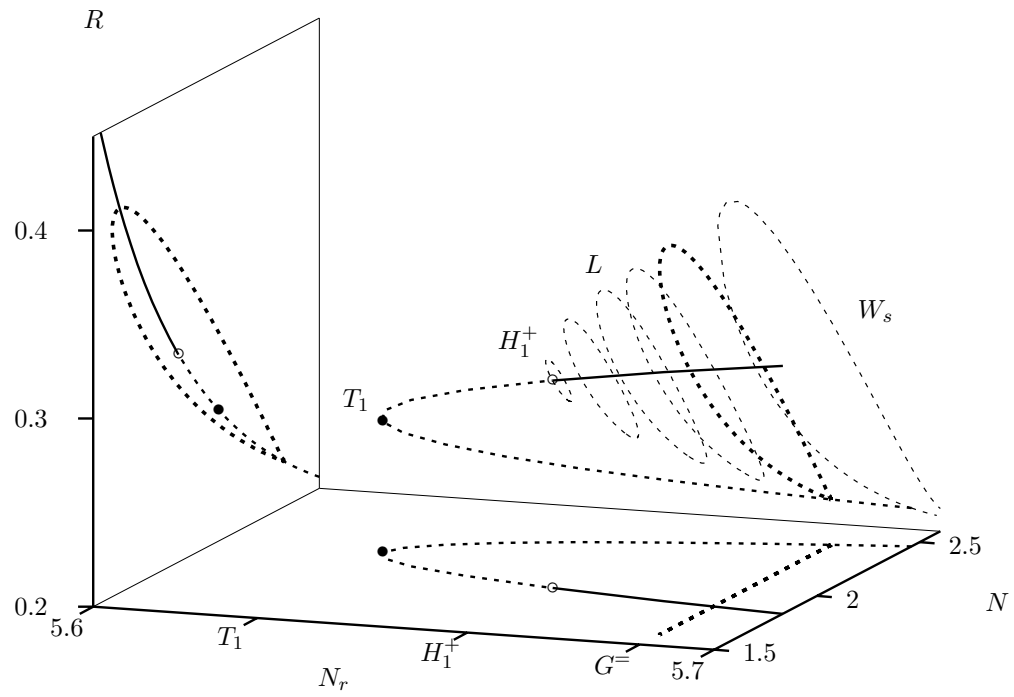

Figure 2: A three dimensional plot for the two state variables N and R and the control parameter N_r where $\delta_R = 0.016$, see also Figure 1. The projection of the left plane is the phase plane. In this plane only the homoclinic loop is drawn. This occurs at the global bifurcation parameter value $G^=$. For parameter values lower than $G^=$ but higher that H_1^+, the unstable limit cycles L for various N_r values are shown. For parameter values higher than $G^=$ the stable manifold W_s of the saddle equilibrium is plotted. This manifold is the separatrix for the stable equilibrium and extinction.

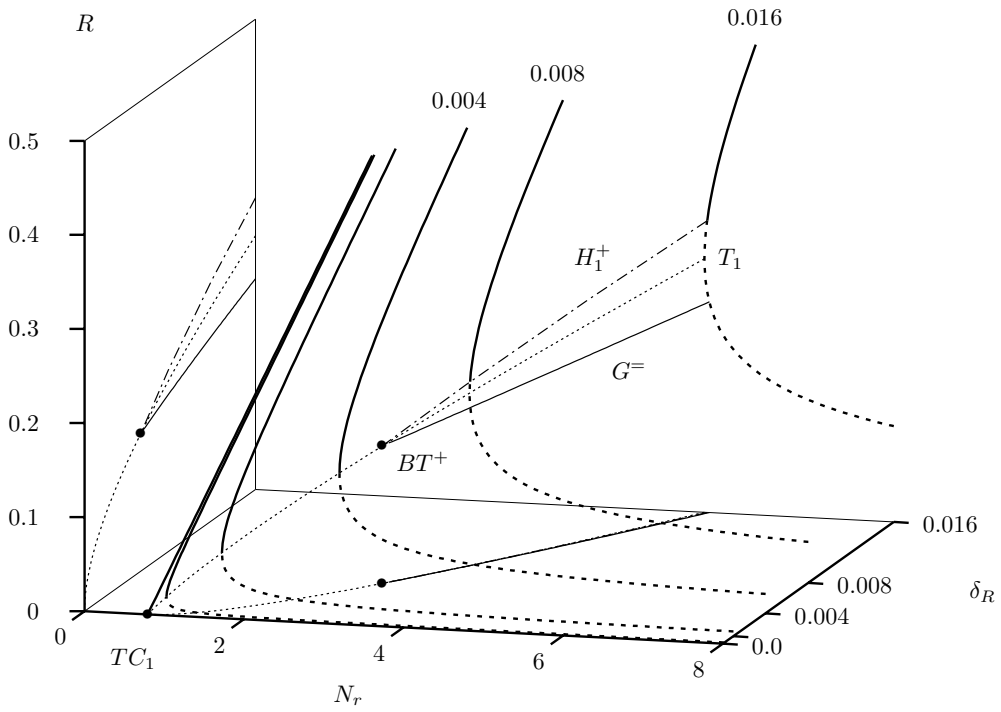

Figure 3: Two one-parameter (R, N_r) and (R, δ_R), and one two-parameter (N_r, δ_R) bifurcation diagrams together in a three dimensional plot for a population (6) in the chemostat. The equilibrium biomass of the resource R is depicted as function of the nutrient level N_r and δ_R. The bifurcations TC_1, T_1 and H_1^+ are the same as in Figure 1. The Bogdanov-Takens codim-two point is denoted by BT^+.

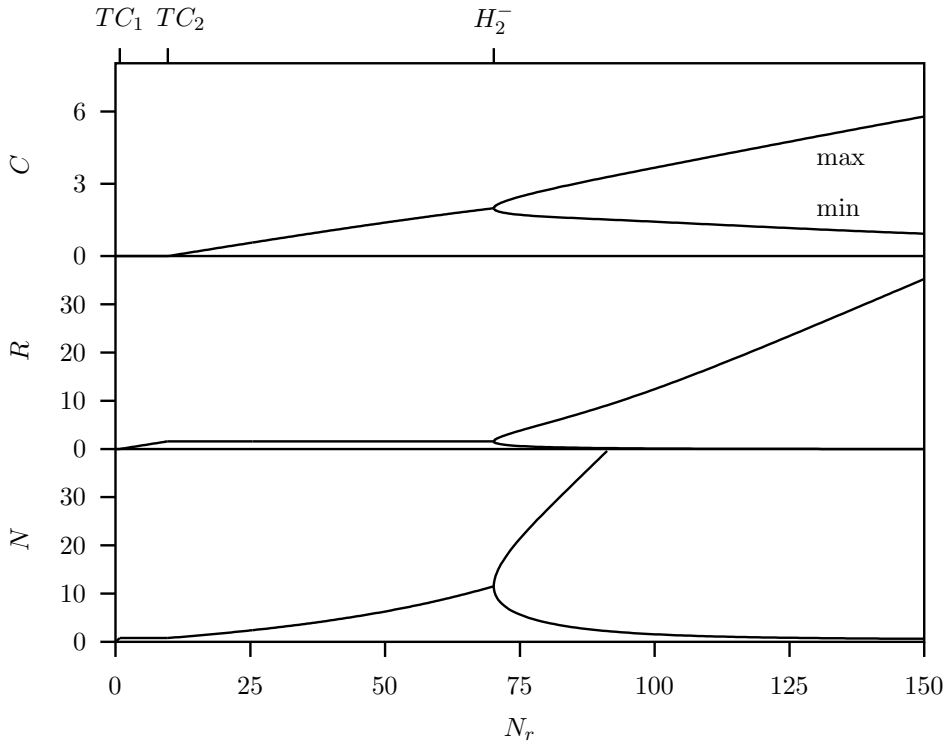

Figure 4: A one-parameter bifurcation diagram for a population (7) in the chemostat. The stationary biomass of the nutrient N, resource R and consumer C is depicted as a function of the nutrient level N_r. For high nutrient levels the system oscillates with extrema indicated.

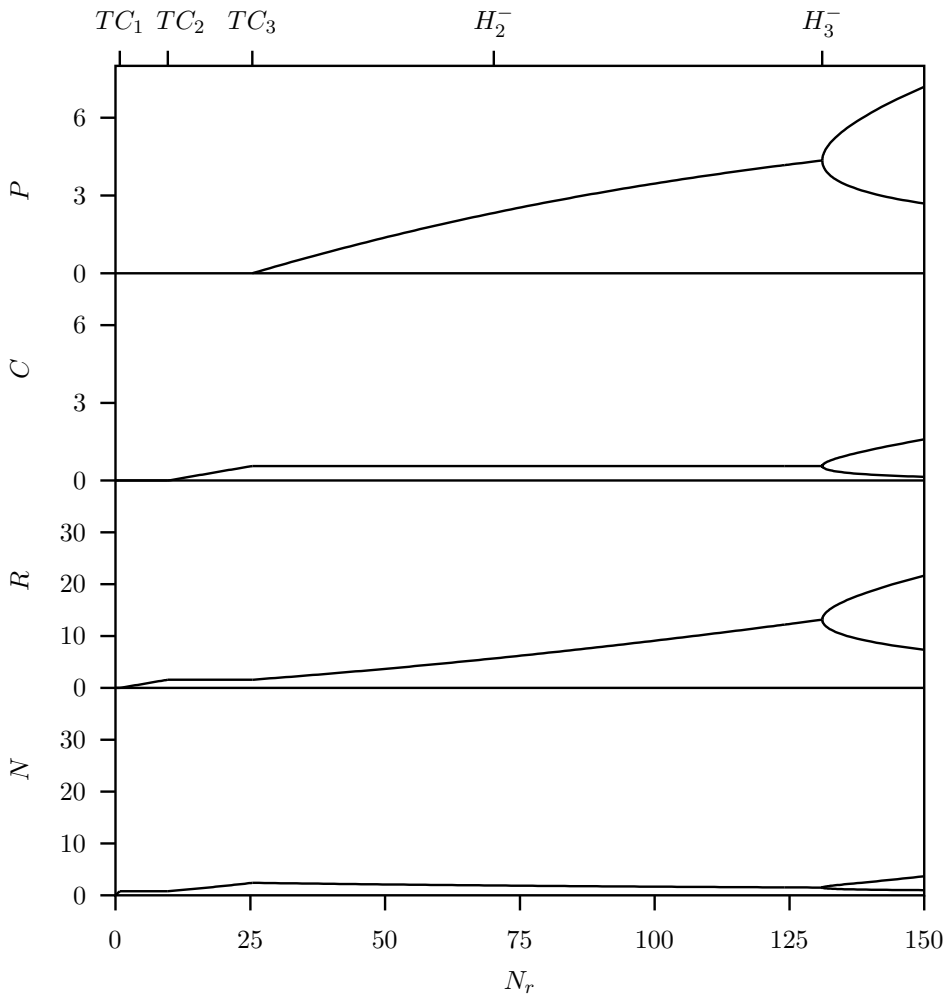

Figure 5: A one-parameter bifurcation diagram for a population (11) in the chemostat. The stationary biomass of the nutrient N, resource R, consumer C and predator P is depicted as a function of the nutrient level N_r. For high nutrient levels the system oscillates with extrema indicated.

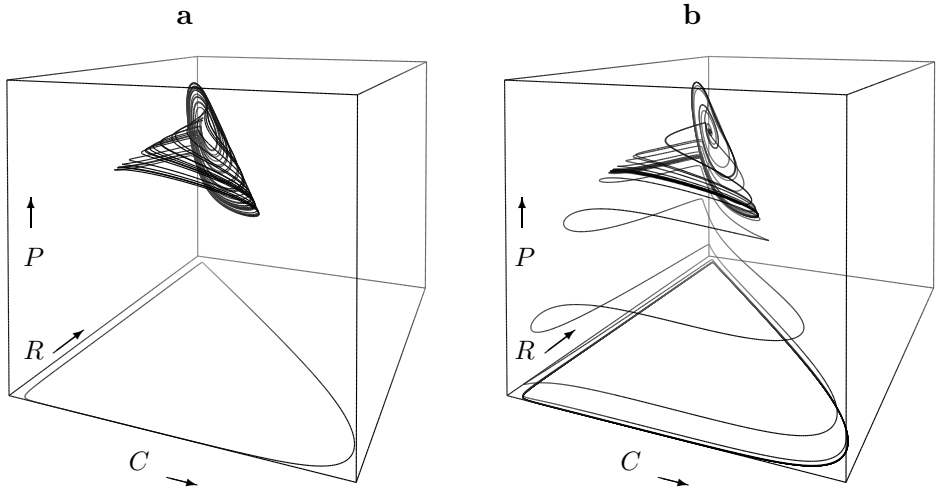

Figure 6: Phase plane plot for system (11) where $m_R = m_C = m_P = 0$ and control parameter values $N_r = 200.0$ and **a**: $D = 0.08732$ and **b**: $D = 0.0873$. For $D = 0.08732$ there are multiple attractors; a chaotic attractor and the attracting limit cycle which is characterised by the absence of the top-predator. The initial condition is chosen so that there is convergence to the chaotic attractor. For $D = 0.0873$ and similar initial conditions the solution follows the "ghost" of a chaotic attractor for a long time before approaching an attractor where the top-predator is absent.

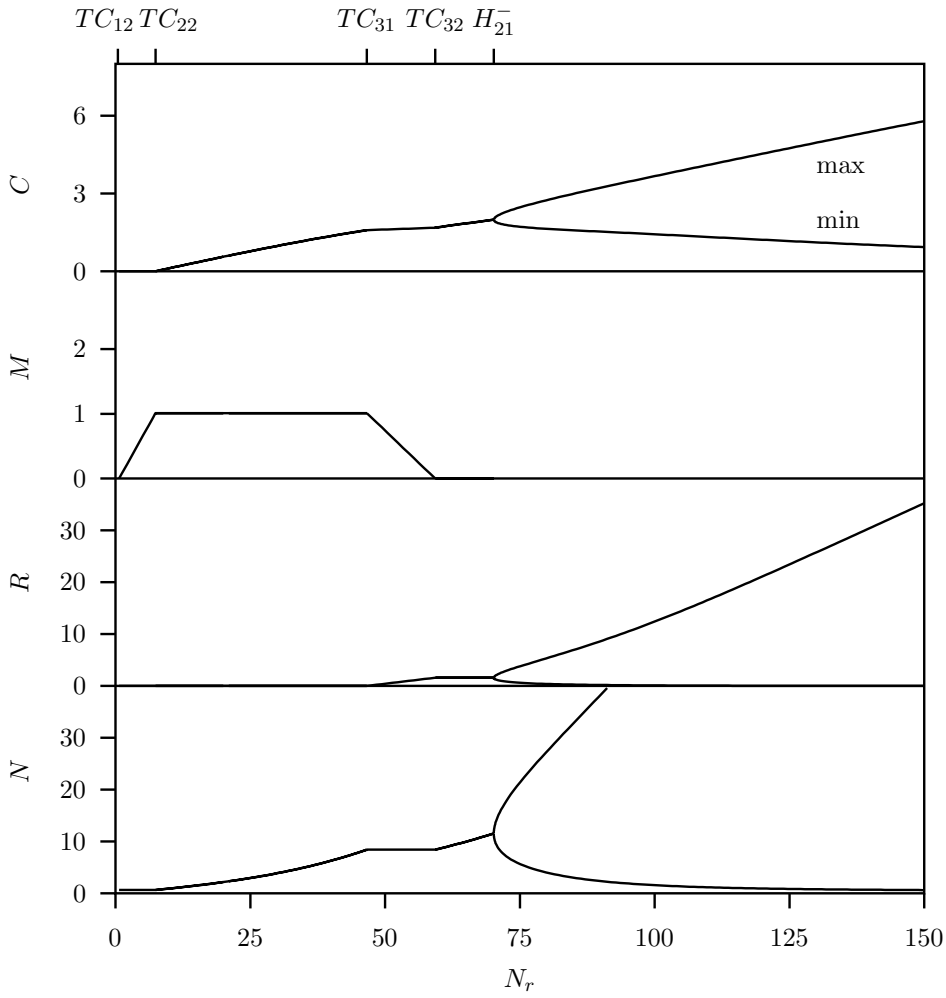

Figure 7: A one-parameter bifurcation diagram for food web (12) in the chemostat. The stationary biomass of the nutrient N, resource R, competitor M and consumer C is depicted as a function of the nutrient level N_r. For high nutrient levels the system oscillates with extrema indicated.

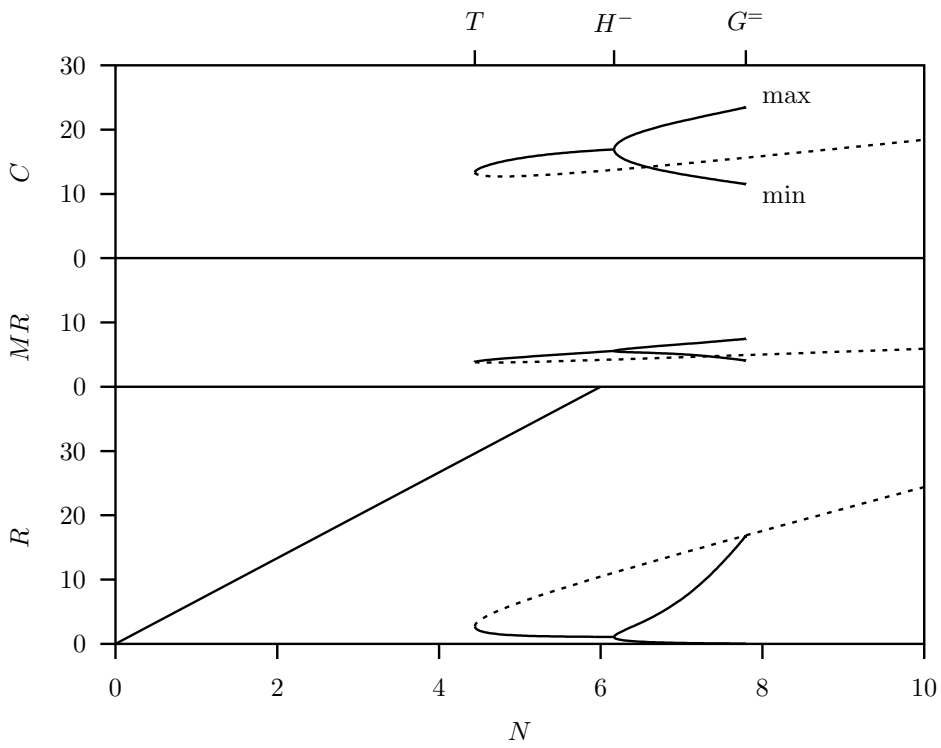

Figure 8: A one-parameter bifurcation diagram for producer–consumer system (13) in a closed environment. The stationary biomass of the producer structural biomass R, producer reserve biomass MR and consumer C is depicted as a function of the total nutrient level in the biota N. Solid lines indicate attractors, the dashed line a saddle equilibrium. For high nutrient levels the system oscillates with extrema indicated. Also the stable equilibrium $M = C = 0$ and $R = N/n_{NP}$ is plotted. Parameters: $m_C = 0.005$ h^{-1}, $n_{NR} = 0.15$ mol/mol , $n_{NC} = 0.25$ mol/mol , $\mu_{MC} = 0.12$ h^{-1} , $\mu_{RC} = 0.075$ h^{-1} , $K_{NR} = 0.15$ mol/mol, $K_{RC} = 10$ mM, $I_{RC} = 0.15$ mol/ (mol h), $\mu_{NR} = 0.25$ h^{-1}, $m_{RC} = 0.002$ h^{-1}, $m_{MC} = 0.001$ h^{-1}.