

Population Dynamics:
General Results from Local Analysis

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Abstract

Mathematical models are frequently used to investigate the dynamics of interacting populations. In these models the biological interactions are usually described by simple mathematical functions. However, simple functions can hardly capture the complexity of biological interactions. The use of simple mathematical functions may therefore result in ecological models of limited validity. This risk can be avoided if general models are used. In general models the mathematical functions that describe the interaction between populations are not specified. As a result a single general model describes a whole class of similar systems at once.

In this thesis a new approach to the formulation and analysis of general models is presented. This approach is used to formulate and study models of general food chains and food webs.

This work illustrates that general models can be analysed in the framework of local bifurcation theory. In particular the computation of Hopf bifurcations provides much information about the local and global dynamics of general models. In order to compute Hopf bifurcations efficiently a special mathematical technique, the method of resultants, is derived.

Application of the method of resultants and the general modelling approach reveals a new, general solution to the famous paradox of enrichment. It is shown that enrichment always destabilizes certain ecological models if the interaction is described by simple functions. However, a large class of more complex functions exists which result in more complex model behaviour. If these functions are used in a model enrichment may have a stabilizing effect. In this way general models explain why enrichment does not generally lead to instability in experiments.

Another question which is much debated is whether chaotic dynamics is possible in ecological systems. While chaos is observed in many models it is believed to vanish if certain biological details are taken into account. The investigation of general models reveals that chaotic parameter regions generally exist in systems with more than three trophic levels. This result holds for a large class of models regardless of the specific details.

The investigation of ecological food webs reveals that a large class of food webs behaves qualitatively similar to food chains. For many purposes it is therefore sufficient to model these food webs as food chains. Furthermore, it is shown that the strong form of the famous competitive-exclusion principle only occurs because of certain degeneracies that exist in simple ecological models.

Zusammenfassung

Zur Untersuchung ökologischer Dynamik werden häufig mathematische Modelle eingesetzt. Viele dieser Modelle beschreiben die Wechselwirkungen zwischen Populationen von Lebewesen mit sehr einfachen mathematischen Funktionen. Diese einfachen Funktionen können die Komplexität ökologischer Prozesse jedoch kaum widerspiegeln. Der Gültigkeitsbereich von Modellen, in denen solche Funktionen verwendet werden, kann deshalb sehr begrenzt sein. Dieses Problem lässt sich vermeiden, wenn nicht spezifische sondern allgemeine Modelle betrachtet werden. In allgemeinen Modellen werden die Funktionen, die die Wechselwirkungen zwischen Populationen beschreiben, nicht spezifiziert. Auf diese Weise kann ein einzelnes allgemeines Modell eine ganze Klasse von spezifischen Systemen auf einmal beschreiben.

In dieser Arbeit wird ein neuer Ansatz zur Formulierung und Analyse allgemeiner Modelle entwickelt. Dieser Ansatz wird dann zur Untersuchung ökologischer Nahrungsketten und Nahrungsnetze eingesetzt.

Diese Arbeit zeigt, dass allgemeine Modelle im Rahmen der lokalen Bifurkationstheorie analysiert werden können. Insbesondere die Berechnung von Hopf-Bifurkationen erlaubt viele Rückschlüsse auf die lokale und globale Dynamik allgemeiner Modelle. Im Rahmen der Arbeit wird eine Methode (das Resultantenverfahren) vorgestellt, die es erlaubt Hopf-Bifurkationen sehr effizient zu berechnen.

Die Anwendung des Resultantenverfahrens und des allgemeinen Ansatzes zeigt eine neue Lösung für das ökologische Anreicherungsparadoxon. Es wird gezeigt, dass eine Anreicherung immer destabilisierend auf ökologische Modelle wirkt, in denen die Wechselwirkung zwischen Spezies mit einfachen Funktionen beschrieben wird. Es existiert jedoch eine große Klasse von Funktionen, die zu komplexerem Verhalten führen. Wenn solche Funktionen verwendet werden, kann eine Anreicherung stabilisierend auf das System wirken. Auf diese Weise zeigen allgemeine Modelle, wieso eine Anreicherung in natürlichen Systemen nicht immer zu einer Destabilisierung führt.

Eine weitere, viel diskutierte Frage ist, ob chaotische Dynamik in ökologischen Systemen auftreten kann. Chaos tritt bereits in sehr einfachen ökologischen Modellen auf. Es wird jedoch vermutet, dass bestimmte Details der ökologischen Wechselwirkungen Chaos verhindern können. Die Analyse allgemeiner Modelle zeigt, dass chaotische Dynamik im Allgemeinen in allen Systemen mit mehr als drei trophischen Stufen auftritt. Dieses Ergebnis gilt für eine große Klasse von Modellen, unabhängig davon welche biologischen Details im einzelnen berücksichtigt werden.

Die allgemeine Untersuchung von Nahrungsnetzen zeigt, dass sich viele Nahrungsnetze äquivalent zu Nahrungsketten verhalten. Für viele Anwendungen ist es deshalb ausreichend solche Nahrungsnetze als Nahrungsketten zu modellieren. Des Weiteren zeigt sich, dass das berühmte Konkurrenz-Ausschluss-Prinzip in seiner starken Form nur auf Grund von gewissen Annahmen gilt, die häufig in einfachen Modellen gemacht werden.

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Chapter 1

Introduction

But is it feasible to express a complete explanation of predation in mathematical languages in view of the complexities that can arise? Any such attempt might well be a very rough approximation with limited application and, once proposed, might stifle further understanding in the face of an apparently inviolate mathematical explanation ...

– C.S. Holling, Ann. Rev. Entomol. 7, 1962.

Our ecological environment is a huge and highly complex system. This complexity arises in part from the diversity of biological species, but also from the complexity of every individual organism. On a small scale the individuals interact by predation, competition or cooperation. On the larger scale the microscopic interactions lead to interactions between populations. The population dynamics is sometimes stationary but can also be periodic, quasiperiodic or chaotic. Invasions, population bursts and extinction are frequently observed. This dynamics is the driving force behind the biological evolution that acts on an even larger scale. In course of the evolution species emerge and vanish in a complicated sequence of succession.

Since the human population is growing, and can be expected to grow in the future, the anthropogenic influence on the environment increases. This influence can induce major changes in the functioning of an ecosystem and cause the extinction of many species. The fact, that biological succession has always taken place illustrates that we can not conserve every single species. But, for ethical as well as economical reasons, major transitions that involve the destruction of whole ecosystems have to be avoided. To stop the anthropogenic influence on the environment altogether is in general impossible and can in many cases likewise lead to the destruction of an ecosystem. Instead, efficient strategies for the conservation of ecosystems are needed. In order to implement such strategies in the face of the complexity of the problem requires a profound understanding of ecosystem functioning.

In the past many interesting insights have been gained from the investigation of simple ecological models. In these models many biological details that contribute to the complexity of nature are neglected. This enables the modeler to study ecological key processes in an abstract, conceptual way. In this way simple models can help us to understand the very building blocks of ecological systems.

The strength of simple models is generality. Simple models do not depend strongly on specific features of the system under consideration. Consider for instance the work of C.S. Holling. In order to describe predation Holling proposed four simple mathematical functions. These functions can be used to model predation between a large range of different species. Models which are based on these simple functions can therefore describe very different ecological systems. Say, for instance the feeding of Lynx on Hare and predation among zooplankton. A more precise model of the interaction of Lynx and Hare could be obtained if more details of the behavior of the individuals were included in the model. However, these specific details would make the generalization of the results to other systems difficult.

While the generality of Holling's insights is impressive, the lines quoted above raise some doubts. Holling asks whether it is really possible to derive an simple mathematical model of the complex process of predation. In fact, every mathematical model is based on certain assumptions. An implicit assumption made in most simple models is that the model describes a *generic* situation. If this assumption is true the dynamics of the model do not depend strongly on the model structure. In this case it is reasonable to assume that biological details that have been neglected in the model will not effect the predictions qualitatively. However, if our model describes a *degenerate* situation, biological details can have a dramatic impact on the predictions of the model. Such models are indeed of "limited application" as Holling puts it. In this light generality is not only an advantage of simple mathematical models but a necessary requirement.

In this work we formulate and analyze general models of ecological food chains and food webs. We avoid to describe ecological processes, like predation, by specific mathematical functions. Instead, general functions are used that are not restricted to a particular functional form. The general models are applied to investigate several questions that are related to the stability of ecological systems.

A question that is hotly debated is whether the dynamics of natural populations can be chaotic (May 1987, Upadhyay et al. 1998, Cushing et al. 2002). While chaos has been observed in ecological experiments (Tilman and Wedin 1991, Cushing et al. 1996). the detection of chaos in nature is generally very difficult (Nychka et al. 1992, Ellner and Turchin 1995, Hanski et al. 1993). In models chaos is easier to detect and is frequently encountered (Hastings and Powell 1991). However, it has been pointed out that the chaotic regions seem to disappear if models are perturbed in a certain way (Ruxton and Rohani 1998, Fussmann and Heber 2002).

The existence of chaos is related to the larger diversity-stability debate. This debate focusses on the effect of species diversity on the stability of a system. Investigations by May (1973) indicate that the stability of food webs generally decreases with increasing diversity. In fact, the famous competitive exclusion principle states that two species which occupy the same ecological niche can not coexist in a stable steady state (Gause 1934, Armstrong and McGehee 1980). However, in contrast to the theoretical results the highly diverse systems observed in nature seem to be very stable while simpler systems often exhibit instability (Odum 1953, Elton 1958, MacArthur 1955). These results indicate that the stability observed in nature is (at least on the species level) not the stability of steady states but persistence in a non-stationary state (McCann 2000). Since the diversity of species on earth is declining the question arises how the diversity and stability of ecological systems are related.

In aquatic systems eutrophication is considered as a major threat to species diversity and ecosystem stability (Tilman et al. 2001). In simple ecological models it is often observed that increasing the supply of nutrients destabilizes the system and leads to the extinction of species (Huffaker et al. 1963, Rosenzweig 1971, Gilpin 1972). This detrimental effect of increased nutrient availability is known as the paradox of enrichment. The destabilizing effect of enrichment was confirmed in experiments by Luckinbill (1974), Tilman and Wedin (1991), Morin and Lawler (1995) However, in other systems enrichment had no destabilizing effect (McAllister et al. 1972, McCauley and Murdoch 1990) or even stabilized the system (Kirk 1998).

In the context of our general models the questions outlined above can be studied with a high degree of generality. Despite this generality the models can be analyzed with the tools of dynamical system theory. In this way the application of general models enables us to draw very general ecological conclusions.

We start in Chap. 2 with a brief review of central concepts of dynamical systems theory. The chapter focuses on the different forms of bifurcations that are encountered in our investigation of ecological models. In particular, we show that Hopf bifurcations play an important role. Hopf bifurcations are in many cases responsible for the destabilization of steady states in ecological models. Furthermore, the interaction between Hopf bifurcations gives rise to bifurcations of higher codimension which indicate complex dynamics.

For the computation of Hopf bifurcations we use the method of resultants. This method is described in detail in Chap. 3. We show how resultants can be applied to the computation of Hopf bifurcations and discuss the advantages of resultants in comparison to other methods. In this work we apply the method to compute the bifurcation diagrams on which the majority of our conclusions is based.

The computation of local bifurcation diagrams can reveal many interesting insights on the system under consideration. We apply this analysis to general models of food chains and food webs. A general food chain model is formulated in Chap. 4. In this model local bifurcations can be computed with a high degree

of generality. We illustrate this analysis by computing bifurcation diagrams for food chain of different length. We identify a key parameter for food chain stability and show that certain bifurcations of higher codimension generically exist in long food chains. These insights form the foundation for the investigation in Chap. 5 and Chap. 6.

In Chap. 5 we study the paradox of enrichment. We apply the results of the general analysis to investigate the effect that enrichment can possibly have on a specific model. Our analysis reveals that enrichment generally destabilizes models in which predation is described by simple functions. However, in more complex models that take more biological details into account enrichment can have a stabilizing effect. We show that more that the stability of steady states depends very sensitively on the functions that are used in a given model. In particular simple models of predator-prey interaction may not be sufficient describe the stability of the natural system correctly.

In Chap. 6 we focus on the existence of chaos in food chains. We show that certain bifurcations of higher codimension appear in long food chains. The presence of these bifurcations proves that all long food chains are in general chaotic in certain parameter regions. We show that these regions survive even if strong nonlinear mortality terms are considered in the model. Moreover, we locate some rare bifurcations of even higher codimension that generally appear in long food chains. The ecological implications of these bifurcations are at present unclear. However, the bifurcations may serve as examples for future mathematical analyses which may reveal additional biological insights.

Finally, in Chap. 7 we extend our general approach to food webs. We derive a general food web model that allows us to compute the local bifurcations of certain food webs with a high degree of generality. Our investigation reveals that competitive exclusion is related to a certain type of degeneracy that appears in some specific models. However, if more biological details are taken into account coexistence is generally possible. Thereafter, we use our general model to investigate the dynamics of food webs with different web geometries. We show that the local dynamics of a large class of food webs is qualitatively identical to the dynamics of food chains. The results of Chap. 5 and Chap. 6 can therefore be extended to a large class of food webs.

We summarize the results of this work in Chap. 8 and describe some perspectives for future investigations. In particular we argue that our general approach can be applied to a large range of problems from different disciplines of science.

Chapter 2

Dynamics and Bifurcations

The purpose of this work is to obtain general insights in the dynamics of ecological populations. This is achieved by applying modern methods from dynamical systems theory.

In this chapter a brief overview over selected topics from the theory of dynamical systems is given. The material presented here is elementary and can be found in most textbooks (Wiggins 1990, Argyris et al. 1994, Glendinning 1994, Kuznetsov 1995, Arrowsmith and Place 1998, Strogatz 2000, Guckenheimer and Holmes 2002). In contrast to these, we focus specifically on bifurcations that appear in the discussion of our ecological models. Most importantly we show that the Hopf bifurcation plays, for various reasons, a crucial role. In effect, this chapter outlines the theoretical framework in which the present work fits. Furthermore, it serves as a motivation for the subsequent chapter which focusses on the computation of Hopf bifurcations.

We start by reviewing important concepts of dynamical systems theory in Sec. 2.1. The central notions of complexity and stability are introduced in Sec. 2.2. Thereafter in Sec. 2.3, we discuss the impact of Hopf bifurcations and related situations on the stability and dynamical complexity of ecological models. Finally, some important points are summarized in Sec. 2.4.

2.1 Dynamical Systems - general definitions

In this section we introduce several key concepts of the theory of dynamical systems. This is done very briefly and without mathematical rigor. The purpose of this section is to provide a conceptual framework. Important points like the question of stability and complexity are discussed in more detail below.

Mathematically speaking, a dynamical system can be defined as a set of prescriptions which determine the time evolution of a set of state variables

(Kuznetsov 1995). The prescriptions will in general depend on a set of (external) parameters and in some cases time.

Dynamical systems are used to model experimental observations in many disciplines of science. In most of these models the prescriptions that govern the time evolution are formulated either in the language of ordinary differential equations (ODEs), partial differential equations (PDEs) or discrete time maps. The resulting equations are in general nonlinear and may be stochastic or deterministic in nature. If time does not appear explicitly in the equations the system is called *autonomous*. In the following we focus on the dynamics of deterministic, autonomous ODE systems.

The models studied here are *dissipative* dynamical systems. In such systems the phase space volume spanned by an ensemble of systems (with different initial conditions) contracts in average as time passes. In dissipative systems we can distinguish between *long term dynamics* which persists even after an arbitrarily long time and *transient dynamics* which is only observed while the system approaches a certain region of phase space on which the long term dynamics takes place.

Using the methods of qualitative analysis the long term dynamics of a given system can be studied directly. A central point of these methods is the concept of invariant sets. A subspace of the phase space is called *invariant set*, if every trajectory starting in the subspace stays in the subspace for all time. An invariant set is *stable* if every trajectory starting close to the set remains close. If the trajectories stay not only close but actually approach the invariant set as time passes by, it is called *asymptotically stable*.

In general the phase space of the system under consideration contains many invariant sets. In the following we mainly consider the dynamics close to invariant sets which do not contain smaller subsets which are also invariant. These sets are called *minimal invariant* or *non-wandering* sets. Sets which attract all trajectories from a neighborhood with positive Lebesgue measure are called *attractors*. Other minimal invariant sets exist which repel neighboring trajectories (*repellers*) or are attracting in some directions and repelling in others (*saddles*).

Depending on the nature of the stable minimal invariant sets the long term dynamics of any ODE system can be either *stationary*, *periodic*, *quasiperiodic* or *chaotic*. Stationary behavior occurs on invariant sets consisting only of a single point in phase space. Such sets are called *steady states*, *fixed points* or *equilibria*. Periodic behavior is encountered on minimal invariant sets consisting of an isolated loop in phase space which is called *limit cycle*. Quasiperiodic dynamics takes place on *invariant tori* which can be two- or three-dimensional. Higher dimensional tori are rarely observed because of the Ruelle-Takens theorem (Ruelle and Takens 1971).

Apart from these “smooth” minimal invariant sets non-smooth sets may be encountered. The dynamics on these *strange* sets is usually chaotic. However, some examples of strange non-chaotic attractors have been found (Grebogi et al. 1984). A safe way to determine the nature of the dynamics on a given attractor is the computation of Lyapunov exponents which is discussed in Chap. 6.

2.2 Dynamical Complexity and Stability

Two central concept around which this work revolves are *complexity* and *stability*. Both terms are widely used and have different meanings in different disciplines of science.

Complexity

The term complexity is frequently used to describe the fact that for a given problem no well established method is applicable (Badii and Politi 1999). More rigorous measures of complexity have been formulated in the context of statistical mechanics, information theory and dynamical systems theory. These measures describe the complexity of temporal, spatio-temporal or spatial patterns.

In the context of ecological systems the term complexity is often used in a different way. The complexity under consideration here is primarily the complexity of the system itself. Ecological systems are complex because of the diversity of biological species as well as the complex nature of their interactions.

In this work we will use the term complexity to describe the ecological complexity found in nature as well as the dynamical complexity of models. In the following, only chaotic dynamics are called complex. Nevertheless we can say that periodic behavior is more complex than stationary behavior. Quasiperiodic behavior is more complex than periodic behavior but less complex than chaotic behavior.

Stability

The term stability is used in ecology to describe the ability of a system to withstand perturbations (Holling 1973). For instance asymptotic stability (c.f. Sec. 2.1) indicates resistance to small perturbations of the state variables. In this work we call a system stable if an asymptotically stable steady state exists. Asymptotic stability is sometimes quantified in the form of *resilience*, which is connected to the return time after a small perturbation. The resistance to larger perturbation of the state variables can not be measured in terms of resilience or asymptotic stability, since large perturbations may cause a system to depart entirely from an asymptotically stable set.

An invariant set to which the systems returns even after arbitrarily large perturbations is called *globally stable*. However, globally stable minimal sets exist only in very few systems.

A much weaker notion is *persistence* which indicates that the boundary of the positive cone of the phase space is repelling. In a persistent system species

will in general survive perturbations of the state variables although the system will not necessarily return to the same attractor.

Apart from perturbations of state variables we have to consider perturbations of parameters and the model structure itself. Such perturbations may result in a transition from one type of dynamical behavior to another one. In ecology variations of parameters are often considered to be *stabilizing* if they cause a transition to less complex dynamics or increase the resilience of the system. In the following we call the variation of a parameter stabilizing if it can not cause a steady state to become unstable, but can possibly stabilize a steady state. Whether a stabilizing variation of a parameter actually causes the stabilization of a steady state will in general depend on the values of other parameters.

Stability of steady states

Let us consider the stability of steady states more closely. The ecological models considered in this work are formulated in the language of ODEs. A general ODE system can be written in the form

$$\dot{X}_n = f_n(X_1, \dots, X_N, p_1, \dots, p_M) \quad n = 1 \dots N, \quad (2.1)$$

where X_1, \dots, X_N is a set of variables. The time evolution is determined by the functions f_1, \dots, f_N depending on the parameters p_1, \dots, p_M . Here N denotes dimension of the phase space while M is the dimension of the parameter space. The values of the variables in the steady state are denoted by X_1^*, \dots, X_N^* .

In order to decide whether a steady state is stable we have to consider small perturbations of the state variables. A linearization of the evolution equations close to the steady state yields the Jacobian matrix. The Jacobian is a real $N \times N$ matrix with the elements

$$J_{ij} = \left. \frac{\partial \dot{X}_i}{\partial X_j} \right|_{\mathbf{x}=\mathbf{x}^*} \quad i, j = 1 \dots N. \quad (2.2)$$

If all eigenvalues of the Jacobian have non-vanishing real parts the steady state under consideration is called *hyperbolic*. A hyperbolic steady-state is asymptotically stable if (and only if) the real parts of all eigenvalues of the Jacobian are negative. Such states are called *stable nodes* or *stable foci*. The term focus is used if complex eigenvalues are present. If eigenvalues with positive real parts as well as eigenvalues with negative real parts exist the corresponding steady state is called a *saddle point*. Sometimes the term *saddle focus* is used to indicate the presence of complex eigenvalues. Steady states in which all eigenvalues have positive real parts are called *unstable nodes* or *unstable foci*.

Transitions in the stability of steady states occur if eigenvalues of the Jacobian cross the imaginary axis in response to the parameter variation.

2.3 Bifurcations in systems of ODEs

Let us now study transitions in the long-term dynamics in a more systematic way. We consider two systems with slightly different parameter values. In

general, the two systems will have different but topologically equivalent phase portraits. However, certain critical parameter values may exist at which the phase portrait changes in a qualitative way. The points in parameter space at which this happens are called *bifurcation points*. Crossing a bifurcation point in parameter space results in a qualitative transition in phase space. This transition is called *bifurcation*.

2.3.1 Properties of Bifurcations

Various types of bifurcations exist. These types differ by the corresponding topological changes in the phase portrait of the system. Consequently, they have different effects on ecological dynamics. Before we enter the discussion of specific types of bifurcations let us introduce some important properties which many bifurcations share. According to these properties the bifurcations can be classified and discussed in a more organized way.

Locality

An important property of bifurcations is locality. Mathematically speaking, a bifurcation is *local* if the topological changes of the phase portrait originate from a single point in phase space (Kuznetsov 1995, Arrowsmith and Place 1998). Bifurcations which are not local are called *global bifurcations*.

According to this definition bifurcations of cycles and tori are always global bifurcations. However, several bifurcations of cycles and tori can be conveniently analyzed in a Poincaré map of the system. In this map certain global bifurcations of the ODE system appear as local bifurcations. In this work we refer to such bifurcations as *local bifurcations of cycles* and *local bifurcation of tori* respectively. The term global bifurcations is only used for bifurcations which do not correspond to local bifurcations of Poincaré maps.

Genericity

All generic bifurcations of a given type are qualitatively similar to a *normal form* for this type of bifurcations. The normal form can be understood as a simple prototype for a certain type of bifurcation. It captures the qualitative features of all possible generic bifurcation of the same type.

In order to be generic a bifurcations has to satisfy a finite number of *genericity conditions* which are formulated as non-equalities. If at least one of the genericity conditions is violated the bifurcation is *degenerate*. The behavior of a degenerate bifurcation will in general differ from the behavior of the normal form.

It has been argued that only generic bifurcations should occur in nature. This view is based on the idea that the probability to violate a genericity condition “by chance” is zero. However, in nature certain symmetries which can enforce degeneracy exist. Even, if no such symmetry is present the system may evolve into a degenerate state. In ecology this can happen if the degenerate situation is evolutionary favorable. Nevertheless, we can expect the generic form of

bifurcations to occur unless some symmetry or mechanism favoring degeneracy is present.

Codimension

In ecological models the time evolution of state variables often depends on a large number of parameters. The equations that govern the time evolution are in general smooth functions of the parameters. Therefore bifurcations do not exist as isolated points in parameter space, but are in general located on manifolds consisting entirely of such points.

The difference between the dimension of the parameter space and the dimension of the manifold on which a certain type of bifurcation occurs is called *codimension* of the bifurcation. In other words, the codimension denotes the number of parameters that have to be varied to find the bifurcation.

For instance, the manifolds on which codimension-1 bifurcations occur are hyper-surfaces in parameter space. In order to find a bifurcation of codimension-1 we have to vary one parameter.

If we vary a second parameter to move along a hypersurface of codimension-1 bifurcations a codimension-2 bifurcation may be encountered. This will in general be the case if two codimension-1 bifurcations involving the same invariant set meet or when certain genericity conditions (*non-degeneracy conditions*) of a codimension-1 bifurcation are broken. The codimension-2 bifurcations occur on hyperlines in parameter space. In a codimension-2 bifurcation the properties of codimension-1 bifurcations change. In this sense codimension-2 bifurcations are bifurcations of bifurcations. If we follow the codimension-2 bifurcations, bifurcations of even higher codimension can be found.

In order to observe a bifurcation of codimension-2 in an experiment one would have to fix one parameter *exactly* at the bifurcation value while another parameter is varied. Any bifurcation of codimension-2 or more can therefore in general not be expected to be observed in a natural system. However, the investigation of bifurcations of higher codimension is still interesting. The codimension-2 bifurcations of a given model reveal valuable information about global dynamics that could otherwise not be obtained with the same degree of generality (cf. Sec. 2.3.4).

2.3.2 Codimension-1 bifurcations of steady states

Let us now discuss some important codimension-1 bifurcations of steady states. We have already shown in Sec. 2.2 that transitions in the stability of steady states occur if eigenvalues of the Jacobian cross the imaginary axis. Since the eigenvalues change in general smoothly as parameters are varied, they become non-hyperbolic as the imaginary axis is crossed.

Since the Jacobian is in general a real matrix. Its eigenvalues are real or form complex conjugate pairs. In the codimension-1 bifurcations only a single eigenvalue or a single pair of eigenvalues is involved. The local codimension-1 bifurcations of steady states are therefore characterized by the presence of a zero eigenvalue or a pair of purely imaginary eigenvalues.

Saddle-Node bifurcation

In general the situation in which a single zero eigenvalue exists corresponds to a *saddle-node bifurcation*. This bifurcation is encountered if two branches of steady states collide in phase space. As the name indicates this type of collision is often observed between a saddle and a node. However, saddle-node bifurcations involving two saddles are also possible. Other names of this bifurcation are *fold bifurcation*, *turning point* or *limit point*.

In the generic saddle-node bifurcation the two steady states vanish in the bifurcation (s. Fig. 2.1). If the system is in a steady state which undergoes a saddle-node bifurcation it will rapidly approach another attractor once the bifurcation has occurred. In this case the system can in general not be restored to the initial state by restoring the initial parameter values. The saddle-node bifurcation is therefore a *sharp* bifurcation.

In natural systems sharp bifurcations should be avoided since the state which is approached after the bifurcation is, as a rule, undesirable (Bazykin 1998). Moreover, the natural state of an ecological system is in general the result of a complex sequence of succession of species. It is therefore generally very difficult if not impossible to return the system to this state.

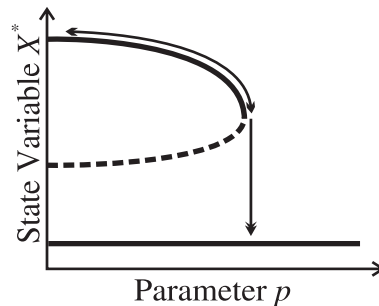


Figure 2.1: In a generic saddle node bifurcation a stable steady state (solid line) collides with a saddle (dashed line). In the bifurcation point both states vanish. Generally, the position of the steady state changes slowly as a parameter p is changed. However, after sharp bifurcations the system rapidly approaches another attractor.

Degenerate Saddle-Node Bifurcations

Above we have discussed the *generic* saddle-node bifurcation. Because of certain symmetries a degenerate form of the saddle-node bifurcation is often encountered in ecological models. This form is called *transcritical* bifurcation (s. Fig. 2.2). In this type of bifurcation two branches of steady states intersect. In contrast to the generic saddle-node bifurcation, both steady states survive the transcritical bifurcation. At the bifurcation point an eigenvalue of the Jacobian of one of the steady states crosses the imaginary axis becoming positive. At the same time an eigenvalue of the other steady state crosses the imaginary axis

becoming negative. The result is an exchange of stability in the direction of the eigenvectors that correspond to the non-hyperbolic eigenvalues.

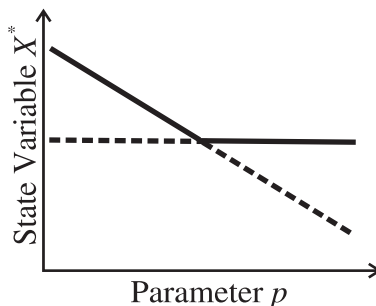


Figure 2.2: Transcritical bifurcations are formed at the intersection of two branches of steady states. In this bifurcation diagram stable steady states are shown as continuous lines. Saddles appear as dashed lines.

Apart from the transcritical bifurcation other degenerate forms of the saddle-node bifurcation exist. Among them are the so-called *pitchfork bifurcation*, in which two new steady states emerge from an existing one and the *three-way transcritical bifurcation* which involves three steady states. Other degenerate situations exist in which an eigenvalue of the Jacobian becomes zero but no bifurcation occurs.

We can distinguish between the generic saddle-node bifurcation and the degenerate forms of this bifurcation by computing the normal form and checking the genericity conditions. In practice it is often easier to compute the steady states and their stability at parameter values close to the bifurcation point.

In the main part of this work we study general ecological models. In these models, steady states can not be computed with the chosen degree of generality. Although normal form analysis is in principle still possible, it is beyond the scope of this work. Nevertheless, we are still able to find the points in parameter space at which zero eigenvalues occur. Furthermore, we can confirm that the transitions which take place in these points are bifurcations. In the following we refer to all codimension-1 bifurcations of steady states, which involve a zero eigenvalue of the Jacobian as *general saddle-node* bifurcations.

Hopf Bifurcations

Although the general saddle-node bifurcations are of some importance the *Hopf bifurcation* (Andronov and Leontović 1939, Hopf 1942) turns out to be far more interesting. In this bifurcation two complex conjugate eigenvalues of the Jacobian cross the imaginary axis. The bifurcation is generic if the axis is crossed at a non-zero velocity.

We can distinguish between *supercritical* and *subcritical* Hopf bifurcations. In the supercritical case a stable limit cycle emerges while the steady state be-

comes unstable. This corresponds to a transition from stationary to oscillatory long-term behavior. By contrast, the subcritical Hopf bifurcation involves an unstable limit cycle which contracts around a stable steady state. At the bifurcation point the limit cycle vanishes leaving the steady state unstable. Since neither limit cycle nor steady state are stable after the bifurcation the system has to approach some other attractor. In contrast to the supercritical case the subcritical Hopf bifurcation is a sharp bifurcation.

The Hopf bifurcation is a very prominent bifurcation. It plays an important role in the dynamics of models from many different disciplines of science. In ecology the Hopf bifurcation is related to interesting effects like the paradox of enrichment which is discussed in Chap. 5. Furthermore, the interaction of Hopf bifurcations with other bifurcations can reveal important insights about global dynamics of the system under consideration.

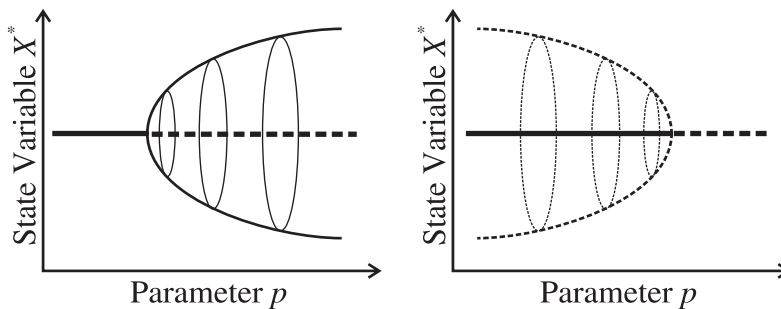


Figure 2.3: In the supercritical Hopf bifurcation (left) a steady state becomes unstable while a stable limit cycle emerges. In the subcritical Hopf bifurcation (right) the steady state stability is lost while an unstable limit cycle vanishes.

2.3.3 Global bifurcations and chaos

In contrast to periodic behavior, chaos can not be reached directly in a local codimension-1 bifurcation of steady states. Instead, the transition from stationary to chaotic behavior will in general involve several and possibly infinitely many bifurcations. In this section we discuss some famous examples for sequences of bifurcations leading to chaos. In this discussion we focus on the routes to chaos which turn out to play an important role in our ecological models. Other famous routes to chaos like Landau chaos (Landau 1944, Hopf 1948), the period doubling cascade (Feigenbaum 1978) and intermittency (Pomeau and Manneville 1980) have been omitted.

Ruelle-Takens chaos

In the Ruelle-Takens scenario a limit cycle emerges from a steady state in a Hopf bifurcation. This limit cycle undergoes a *Neïmark-Sacker bifurcation*

(Neĭmark 1959, Sacker 1965) in which a two-torus emerges. The Neĭmark-Sacker bifurcation is also called *Hopf bifurcation of cycles*. Subsequently, another Hopf-like bifurcation occurs in which a three-torus emerges. The quasiperiodic dynamics on a three-torus is in general structurally unstable (Ruelle and Takens 1971). As a result, any small perturbation leads to chaotic dynamics. The reason for this instability is the formation of complex homoclinic and heteroclinic structures on the surface of the torus. A *homoclinic* orbit is a trajectory that approaches the same saddle in both directions of time. Likewise, a *heteroclinic* orbit is a closed trajectory that connects two or more saddles.

Shil'nikov chaos

The formation of a homoclinic orbit is called *homoclinic bifurcation*. Even if no torus is present, a chaotic attractor can emerge from the homoclinic bifurcation (Shil'nikov 1968, 1970). In general limit cycles are formed (or vanish) in the homoclinic bifurcation. The stability and number of the limit cycles depends on the so-called *saddle quantity* which is the sum of the real parts of the smallest positive eigenvalue and the largest negative eigenvalue of the Jacobian. Homoclinic bifurcations taking place on saddles with negative saddle-quantity give rise to one stable limit cycle. If the saddle index is positive unstable cycles emerge. The number of the unstable cycles created in this way depends on the nature of the saddle. If the bifurcation takes place on a real saddle only one saddle cycle is created. However, an infinite number of saddle cycles can emerge from a homoclinic bifurcation on a saddle-focus. These saddle cycles form a chaotic attractor.

Quasiperiodic chaos

Another scenario leading to the formation of a chaotic attractor is described by Rand et al. (1982) and Feigenbaum et al. (1982). In this case the chaotic attractor is formed from a two-torus which folds in several places. As a result, the smoothness of torus's surface is lost.

All of the examples discussed above involve the formation of limit cycles. In many cases these cycles emerge from Hopf bifurcations. Being a local bifurcation of steady states the Hopf bifurcation is relatively easy to compute. However, the subsequent bifurcations on the way to chaos are global bifurcations (e.g. homoclinic or heteroclinic bifurcations) or local bifurcations of cycles (e.g. period doubling bifurcations, Neĭmark-Sacker bifurcations or fold bifurcations of cycles). The analytical computation of global bifurcations is only possible in very special examples. In principle local bifurcations of cycles and tori can be computed analytically if the corresponding Poincaré maps are known. However, in order to construct the Poincaré map the ODEs have to be integrated. Analytically, this is again only possible for very few systems. Therefore, global bifurcations as well as local bifurcations of cycles and tori have to be computed numerically in most systems. However, numerical bifurcation analysis can only be applied to specific models. For the general models studied in this work no

numerical approaches exist. However, certain insights in the global dynamics of a given model can be obtained analytically by investigation of codimension-2 bifurcations of steady state.

2.3.4 Codimension-2 bifurcations of steady states

Like codimension-1 bifurcations the codimension-2 bifurcations can be analyzed by derivation of a suitable normal form. We do not go through the details of this analysis here, but quote some important results. A more detailed treatment can be found in (Kuznetsov 1995). In our discussion we focus on the codimension-2 bifurcations which appear in our general population model (s. Chap. 4). Other codimension-2 bifurcations like the well known cusp bifurcation or the Bautin bifurcation have been omitted. The most attention is devoted to the double Hopf bifurcation which turns out to play a crucial role.

Takens-Bogdanov bifurcation

Let us start by considering the *Takens-Bogdanov* (TB) bifurcation (Takens 1974, Bogdanov 1981). This bifurcation is formed on a hyperline in parameter space on which a Hopf bifurcation meets a general saddle-node bifurcation. If we approach the TB bifurcation on the Hopf bifurcation the symmetric, purely imaginary eigenvalues approach zero. In the TB bifurcation point a double zero eigenvalue exists. At this point the Hopf bifurcation vanishes (cf. Fig. 2.4). Beyond the TB bifurcation a hyper surface exists on which we find a symmetric but purely real pair of eigenvalues. We call such a constellation of eigenvalues *pseudo Hopf situation*. In literature the term *real Hopf bifurcation* is frequently used. We avoid this term because of possible confusions with the “real” Hopf bifurcation which is also called *imaginary Hopf bifurcation*. The pseudo Hopf situation is technically no bifurcation since no topological changes in the phase portrait occur. However, it is still of some interest since it can involve a change of the sign of the saddle-quantity.

Apart from the Hopf bifurcation and pseudo Hopf situation at least one homoclinic bifurcation emerges from the TB bifurcation. The limit cycle that emerges from the Hopf bifurcation vanishes in this homoclinic bifurcation.

Since the TB-bifurcation is a codimension-2 bifurcation, it can not be expected to be observed directly in ecological observations. However, the existence of a TB bifurcation in a given ecological model proves that a pseudo Hopf bifurcation and a homoclinic bifurcation have to exist. For the homoclinic bifurcation this is particularly interesting since it is generally difficult to compute directly. In ecological models sudden population bursts can often be observed close to a homoclinic bifurcation.

Gavrilov-Guckenheimer bifurcation

Let us now consider the case in which we have a zero eigenvalue in addition to a purely imaginary pair of eigenvalues. This situation is called *Gavrilov-Guckenheimer bifurcation* (GG) or *zero Hopf bifurcation* (Guckenheimer 1981).

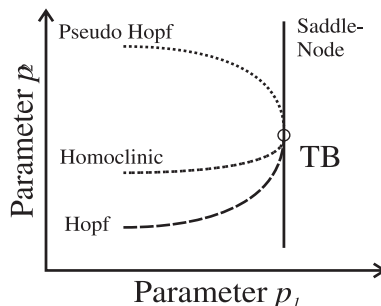


Figure 2.4: A Takens-Bogdanov bifurcation (TB, circle) is formed by the interaction of Hopf and Saddle-Node bifurcations. The branch of Hopf bifurcations ends in the TB bifurcation. A branch of homoclinic bifurcations and a branch of pseudo Hopf situations emerge from the TB bifurcation.

Like TB bifurcations, GG bifurcations are formed by the interaction of Hopf and saddle-node bifurcation surfaces. However, the Hopf bifurcation does not vanish in the GG bifurcation. In comparison to the TB bifurcation the GG bifurcation is much more complicated and can not be plotted in a single two-parameter bifurcation diagram. However, it has been shown that an invariant torus exists close to a generic GG bifurcation. This torus is created in a Neimark-Sacker bifurcation, which emerges from the GG bifurcation. Furthermore, a homoclinic bifurcation leading to the formation of a chaotic attractor has been shown to exist under certain conditions.

For our ecological models the presence of a GG bifurcation implies the existence of regions in parameter space in which quasiperiodic dynamics can be found. Furthermore we can say, that chaotic dynamics is likely to be found close to a generic GG bifurcation.

Double Hopf bifurcation

The *double Hopf* (DH) bifurcation is formed by the interaction of two Hopf bifurcation. The bifurcation is characterized by the presence of two pairs of purely imaginary eigenvalues (Gavrilov 1980, Kuznetsov 1997). Like in case of the GG bifurcation, a branch of Neimark-Sacker bifurcations emerges from the DH bifurcation. The tori that are created in this bifurcation exist only close to the DH bifurcation. Farther away they undergo global bifurcations and vanish. Chaotic regions have been shown to emerge from torus decay or through heteroclinic and homoclinic bifurcations. Other routes to chaos are believed to exist close to DH bifurcations, but have not been investigated in detail. Guckenheimer and Holmes (2002) write that “detailed studies will probably have to await the added stimulus of specific examples in physical applications”. In this light the computation of double Hopf bifurcations is not only interesting from a biological, but also from a mathematical point of view.

Although the routes that lead to the formation of chaos have not been studied in detail, the generic existence of a chaotic parameter region close to the double Hopf bifurcation can be proved. For the purpose of illustration we can loosely describe the situation as follows: In the double Hopf bifurcation four non-hyperbolic eigenvalues exist. The critical eigenspace on which the dynamics close to the bifurcation takes place is four dimensional. In this eigenspace three-tori do generally exist from which chaotic regions emerge because of the Ruelle-Takens theorem. More rigorous mathematical arguments for the existence of chaotic regions are given by Kuznetsov (1995).

2.4 Hopf bifurcations in ecology

In this chapter we have reviewed several key concepts from dynamical systems theory. These concepts form the framework for the analysis of ecological dynamics around which this work revolves. The investigations that are presented in the following are to a large extent based on the computation of Hopf bifurcations.

Hopf bifurcations are often involved in the destabilization of steady states in ecological models. In this way the Hopf bifurcations are connected to many interesting ecological effects like the paradox of enrichment which is discussed in Chap. 5. Furthermore, Hopf bifurcations play a prominent role in the formation of higher codimension bifurcations. Although these bifurcations can not be observed directly in nature, their presence in models proves the existence of certain global bifurcations and local bifurcations of cycles. Most importantly the double Hopf bifurcation can serve as an indicator of chaotic dynamics. In a similar way the Gavrilov-Guckenheimer bifurcation indicates that chaotic dynamics is likely.

In the following the computation of Hopf bifurcations is used to obtain insights in local and global aspects of ecological dynamics. The method by which this computation is performed is discussed in the next chapter.

Chapter 3

Computation of Hopf bifurcations

In Chap. 2 we have argued that Hopf bifurcations play a very prominent role in ecological dynamics. In the following chapters we will study many examples which underline the importance of Hopf bifurcations. The bifurcation diagrams on which our conclusions are based have been generated by employing the so-called *method of resultants*.

In the context of bifurcation theory the method of resultants has been proposed by Guckenheimer et al. (1997). Although the method has in principle been known for a long time it has rarely been used because of certain numerical disadvantages. Today the method is widely unknown and is absent from textbooks on bifurcation analysis.

We have reinvented the method of resultants independently and extended it in several ways. Most importantly, we use the method not in a numerical, but in an analytical, computer-algebra assisted approach. The method has been successfully applied to ecological models and to systems from other disciplines of science. Our results show that, applied in this way, the method of resultants is a very powerful tool.

In order to draw a wider interest to the method we have discussed it from an applicants point of view in (Gross and Feudel 2004b). The discussion presented here follows to a large extend the lines of this paper.

We start by describing several common methods for the computation of Hopf bifurcations in Sec. 3.1. The method of resultants is introduced in Sec. 3.2. In particular we derive analytical conditions for Hopf bifurcations and related situations. Although our main focus is on ODE systems the extension of the method of resultants to maps is studied briefly in Sec. 3.3. Finally, we discuss advantages and disadvantages of the method of resultants in comparison to others methods in Sec. 3.4.

3.1 Computation of Hopf bifurcations

In the past a large number of methods for the computation of Hopf bifurcations has been proposed. Among them we can distinguish between *direct* and *indirect* methods.

Indirect methods

In a typical indirect method one follows a branch of steady states while a parameter is varied. The spectrum of the Jacobian is computed at certain points in parameter space. These points are in general chosen according to some scheme which approximates the bifurcation point (Broyden 1965). The parameter value at which the purely imaginary pair that characterizes the Hopf bifurcation exists is then found by interpolation. Once a bifurcation point has been found, the manifold on which the bifurcation points are located can be followed by numerical continuation (Seydel 1991).

A conceptual drawback of indirect methods is that the eigenvalues have to be computed. In a system of dimension N the Jacobian is a $N \times N$ matrix. In order to compute the eigenvalues of this matrix we have to factorize a polynomial of order N . Analytically, the factorization of polynomials is in general tedious for $N > 2$ and impossible for $N > 4$. The application of indirect methods is therefore limited to numerical bifurcation analysis. Nevertheless, indirect methods are widely used since highly stable algorithms for the computation of eigenvalues exist. The most common indirect methods are the so-called QR-factorization for small systems and the Krylov subspace technique for larger systems (Moore et al. 1990, Chu et al. 1994).

Bordered matrix methods

The efficiency of indirect methods suffers from the fact that they actually solve a much harder problem. Many eigenvalues at several points of parameter space are computed while only one pair of eigenvalues at one point of parameter space is asked for. This inefficiency is avoided in direct methods. In a direct method a system of equations that can be solved directly for the bifurcation point is constructed. In many cases this is accomplished by augmenting the system with additional equations. As a result a bordered matrix is obtained which contains the original Jacobian as well as additional (border) elements.

Two early bordered matrix methods have been proposed by Kubiček (1979, 1980). In these methods two additional variables are introduced which describe the purely imaginary eigenvalues.

A major drawback is that the bordered matrix methods are numerically less stable than indirect methods. To consider the eigenvectors as well as the eigenvalues improves the stability of the method and its efficiency in continuation problems. In most later methods the system is therefore augmented by conditions describing the eigenvalues as well as the corresponding eigenvectors. As a result the dimension of the system grows to at least $2N + 1$ (Griewank and Reddien 1983, Roose and Hlavaček 1985, Roose 1985, Holodniok and Kubiček

1984, Werner 1996).

In practice bordered matrix methods are widely used and are implemented in most software packages for numerical bifurcation analysis (Doedel and Kernévez 1986, Back et al. 1992, Feudel and Jansen 1992, Kuznetsov and Levitin 1996, Doedel et al. 1997). From the computational point of view the additional complexity that is introduced by computing the eigenvectors in the bifurcation point is only a minor drawback. In many cases the knowledge of eigenvectors is desired anyway for normal form computation or as a starting point for the continuation of the emerging limit cycle. However, the size and complexity of the bordered matrices makes them unsuitable for analytical solution.

Classical methods

For analytical computation of Hopf bifurcations the so-called classical methods are more suitable. The mathematical insights on which these direct methods are based date back to the 19th century (Clifford 1868, Hurwitz 1895, Stéphanos 1900). An overview of classical methods is given by Fuller (1968).

One of the methods discussed therein is the well-known Routh-Hurwitz criterion. This criterion has been implemented in the software LinLBF (Khibnik 1990).

Two other criteria presented by Fuller (1968) are based on Kronecker products and bialternate products of matrices. The Kronecker product yields a condition which involves a full determinant of size N^2 . This method is therefore very difficult to apply.

In comparison the bialternate product method yields smaller, more sparsely populated matrices. This method has been studied in the context of bifurcation theory by Fuller (1968), Guckenheimer et al. (1997) and Govaerts (2000). In a given dynamical system with Jacobian \mathbf{J} a center symmetric pair of eigenvalues exists if $|2\mathbf{J} \otimes \mathbf{I}|$ vanishes. In this equation \otimes denotes the bialternate matrix product and \mathbf{I} is the identity matrix of size N . The determinant is of size $N(N-1)/2$ and consists of elements which are polynomials of up to second order of the elements of the Jacobian.

For analytical computations the complex structure and the size of the determinant (which still grows as N^2) are disadvantageous. A numerical approach based on the bialternate product has been implemented in the software CONTENT (Kuznetsov and Levitin 1996).

3.2 The method of resultants

In the previous section several methods for the computation of Hopf bifurcations have been discussed. By contrast, this section is devoted to a more detailed discussion of one specific method. In the following this method is called the *method of resultants*.

Our original derivation of the method was not based on resultants. Instead, it was shown by induction that conditions of a certain form can be used to compute Hopf bifurcations. A closer inspection of these criteria revealed, that the

conditions can be written in determinant form. This yields Sylvester resultants, which are explained in detail below. In the discussion presented here we use the theory of resultants. In this way the conditions for Hopf bifurcations can be derived in a more direct way.

3.2.1 A testfunction for symmetric eigenvalues

Our first aim is to derive a testfunction that detects situations in which center symmetric eigenvalues

$$\lambda_a = -\lambda_b \quad (3.1)$$

are present. The eigenvalues $\lambda_1, \dots, \lambda_N$ of the Jacobian \mathbf{J} are roots of the Jacobian's characteristic polynomial

$$P(\lambda) = |\mathbf{J} - \lambda \mathbf{I}| = \sum_{n=0}^N c_n \lambda^n = 0, \quad (3.2)$$

where c_0, \dots, c_N are constant polynomial coefficients. The two center symmetric eigenvalues λ_a and λ_b have to satisfy Eq. (3.1) as well as

$$P(\lambda_a) = \sum_{n=0}^N c_n \lambda_a^n = 0, \quad (3.3)$$

$$P(\lambda_b) = \sum_{n=0}^N c_n \lambda_b^n = 0. \quad (3.4)$$

By applying Eq. (3.1) the second equation can be written as

$$P(\lambda_b) = \sum_{n=0}^N c_n (-1)^n \lambda_a^n = 0. \quad (3.5)$$

We form the sum and the difference of Eq. (3.3) and Eq. (3.5). This yields

$$\sum_{n=0}^N c_n (1 + (-1)^n) \lambda_a^n = 0, \quad (3.6)$$

$$\sum_{n=0}^N c_n (1 - (-1)^n) \lambda_a^n = 0. \quad (3.7)$$

Note that, Eq. (3.6) contains only terms of even order in λ_a while only odd orders of λ_a appear in Eq. (3.7). To remove the odd orders altogether we assume $\lambda_a \neq 0$ and divide Eq. (3.7) by λ_a . As a result we obtain

$$\sum_{n=1}^N c_n (1 - (-1)^n) \lambda_a^{n-1} = 0. \quad (3.8)$$

This equation contains only even orders of λ_a . The order of the polynomials can now be reduced by defining

$$\chi := \lambda_a^2. \quad (3.9)$$

The quantity χ is called *Hopf number*. Using Eq. (3.9) the conditions Eq. (3.6) and Eq. (3.8) can be written as

$$\sum_{n=0}^{N/2} c_{2n} \chi^n = 0, \quad (3.10)$$

$$\sum_{n=0}^{N/2} c_{2n+1} \chi^n = 0. \quad (3.11)$$

where $N/2$ has to be rounded up or down to an integer value as required.

Using the symmetry condition Eq. (3.1) we have managed to split the characteristic polynomial into two polynomials of half order. By doing so, we have simplified the computation of center symmetric eigenvalues considerably. Instead of having to factorize a polynomial of order N , we can now check for the existence of common roots of two polynomials of the order $N/2$. In contrast, to explicit analytical factorization, which is only possible for polynomials of order $N \leq 4$, common roots of two polynomials can in general be computed regardless of the order of the polynomials.

Two polynomials have a common root if their resultant vanishes (Gelfand et al. 1994). Using the Sylvester formula, the resultant R of the polynomials Eq. (3.10) and Eq. (3.11) can be written as a Hurwitz determinant of size $(N-1) \times (N-1)$. This yields

$$R := \begin{vmatrix} c_1 & c_0 & 0 & 0 & \dots & 0 & 0 \\ c_3 & c_2 & c_1 & c_0 & \dots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ c_N & c_{N-1} & c_{N-2} & c_{N-3} & \dots & c_1 & c_0 \\ 0 & 0 & c_N & c_{N-1} & \dots & c_3 & c_2 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ 0 & 0 & 0 & 0 & \dots & c_N & c_{N-1} \end{vmatrix}, \quad (3.12)$$

where we have for the sake of simplicity assumed that N is odd.

The resultant can be constructed by following a simple algorithm: Take a determinant of size $(N-1) \times (N-1)$. Fill the first element of the first row with c_1 . If the first element of a given row is c_n the first element of the next row is c_{n+2} . If an element is c_n the next element in the same row is c_{n-1} . Use

these rules to fill the whole determinant. Finally, set all coefficients that do not appear in the characteristic polynomial (e.g. c_{-1}) to zero. For instance the resultant for $N = 6$ is

$$R = \begin{vmatrix} c_1 & c_0 & 0 & 0 & 0 \\ c_3 & c_2 & c_1 & c_0 & 0 \\ c_5 & c_4 & c_3 & c_2 & c_1 \\ 0 & c_6 & c_5 & c_4 & c_3 \\ 0 & 0 & 0 & c_6 & c_5 \end{vmatrix}. \quad (3.13)$$

In comparison to the bialternate product the Sylvester resultant yields a much smaller determinant. This advantage is gained at the cost of having more complex terms (in this case the polynomial coefficients) as elements of the determinant. Using other forms of resultants like for example the Bezout resultant or the Companion matrix the size of the determinant can be decreased further at the cost of having even more complex entries.

3.2.2 Bifurcations involving symmetric eigenvalues

In Sec. 3.2.1 we have shown that resultants can be used as a testfunction for center symmetric eigenvalue pairs. Let us now assume that the resultant R vanishes. It is a major advantage of the method of resultants that the corresponding Hopf number χ can in general also be calculated.

A major advantage of the method of resultants is that the Hopf number can be computed from subresultants. These subresultants can be constructed by following a simple algorithm: For systems with $N > 3$, delete the last two columns and the last row of the matrix in R (cf. Eq. (3.12)). This yields a $(N-3) \times (N-2)$ matrix \mathbf{A} . Now we obtain the $(N-3) \times (N-3)$ matrix \mathbf{B} by deleting an arbitrary row j (say, 1) of \mathbf{A} . Form the another $(N-3) \times (N-3)$ matrix \mathbf{C} by deleting the row $j+1$ of the matrix \mathbf{A} . The Hopf number can now in general be written as a quotient of determinants

$$\chi = -\frac{|\mathbf{B}|}{|\mathbf{C}|}. \quad (3.14)$$

We consider the example $N = 6$ again which yields (for $j = 1$)

$$\chi = -\frac{\begin{vmatrix} c_1 & c_0 & 0 \\ c_5 & c_4 & c_3 \\ 0 & c_6 & c_5 \end{vmatrix}}{\begin{vmatrix} c_3 & c_2 & c_1 \\ c_5 & c_4 & c_3 \\ 0 & c_6 & c_5 \end{vmatrix}}. \quad (3.15)$$

For systems with $N = 3$ or $N = 2$ the Hopf number is simply

$$\chi = -\frac{c_0}{c_2}. \quad (3.16)$$

Once the Hopf number has been found we can compute the center symmetric eigenvalues

$$\lambda_{a,b} = \pm\sqrt{\chi}. \quad (3.17)$$

Based on the value of the Hopf number we can distinguish four different situations, which are discussed in more detail below.

Hopf bifurcation

Assume that the resultant R vanishes in a given steady state. If the Hopf number χ is negative, a purely imaginary pair of eigenvalues exists. We can say that a point in parameter space p^* is a Hopf bifurcation point if and only if

$$\begin{aligned} R(p^*) &= 0, \\ \chi(p^*) &< 0. \end{aligned} \quad (3.18)$$

The Hopf bifurcation is generic if the eigenvalues cross the imaginary axis with nonzero velocity. This is the case if

$$\left. \frac{\partial R(p)}{\partial p} \right|_{p=p^*} \neq 0. \quad (3.19)$$

Takens-Bogdanov bifurcation

If the resultant as well as the Hopf number vanish in a given bifurcation we have a double zero eigenvalue. This case corresponds to a codimension-2 Takens-Bogdanov bifurcation.

At first glance it seems strange that the method of resultants works in this case since we had to divide by λ_a to obtain Eq. (3.8). A closer inspection of the equations reveals the following: If λ_a vanishes the conditions Eqs. (3.3), (3.4) are not strictly equivalent to Eqs. (3.10), (3.11). A single zero eigenvalue solves the conditions Eqs. (3.3), (3.4), but not the conditions Eqs. (3.10), (3.11). However, multiple zero eigenvalues, solve Eq. (3.3), (3.4) as well as Eq. (3.10), (3.11). The method of resultants can therefore be used to compute Takens-Bogdanov bifurcations, but not saddle-node bifurcations.

Pseudo Hopf situation

Let us now consider a steady state in which the resultant vanishes, but the Hopf number is positive. In this case the Jacobian has two purely real, center symmetric eigenvalues. This is the case in the pseudo Hopf situation that we have described in Chap. 2.

Complex Hopf situations

We have said that the Hopf number that corresponds to a center symmetric eigenvalue pair can in general be found by computing the quotient of certain sub resultants. However, this approach is doomed to fail if more than one center symmetric pair of eigenvalues exists. In this case the numerator and the denominator of the quotient in Eq. (3.9) vanish and the Hopf number χ is

undetermined. We refer to the situations in which this is the case collectively as *complex Hopf situations*.

Complex Hopf situations are in general of higher codimension. We can therefore expect that the Hopf number can be computed anywhere except on certain hyperlines in parameter space.

One can think of several types of complex Hopf situations. The most important one is the double Hopf bifurcation, which has been discussed in Sec. 2.3.4. Other complex Hopf situations include for instance the Hopf bifurcation on a 1:1-resonant saddle or the codimension-3 Takens-Bogdanov-Hopf bifurcation in which two zero and two purely imaginary eigenvalues exist.

Hopf Number	Eigenvalues (EVs)	Bif. situation
negative	2 purely imaginary EVs	Hopf bifurcation
positive	2 symmetric real EVs	pseudo Hopf situation
zero	double zero EV	Takens-Bogdanov bif.
undetermined	more than 2 symmetric EVs	more complex situation (e.g. double Hopf bif.)

Table 3.1: Four different situations in which the resultant vanishes.

3.3 Extension to Hopf bifurcations in maps

In this chapter we have focused on the computation of Hopf bifurcations in systems of ODEs. However, resultants can be used to compute other bifurcations in a similar way.

The extension of the method of resultants to Hopf bifurcations in maps is particularly interesting. In ecology maps turn up as models of populations with non-overlapping generations (May 1976) or as Poincaré maps of differential equation systems.

In systems of maps fixed points can be defined analogously to steady states in ODEs. In a given fixed point a Hopf bifurcation occurs if a pair of complex conjugate eigenvalues crosses a unit circle around the origin of complex plane. The bifurcation is characterized by the presence of a pair of eigenvalues with

$$\lambda_a \lambda_b = \lambda_a \lambda_a^\dagger = 1. \quad (3.20)$$

This condition is analogous to the symmetry condition Eq. (3.1). By applying it in a similar way we obtain a system of coupled polynomials

$$\sum_{n=0}^N c_n \lambda_a^n = 0, \quad (3.21)$$

$$\sum_{n=0}^N c_n \lambda_a^{N-n} = 0. \quad (3.22)$$

These conditions are analogous to Eqs. (3.3), (3.4). Note however, that in Eq. (3.22) the order of characteristic polynomial coefficients is reversed, while in Eq. (3.4) the signs of the odd terms had been inverted.

We can use resultants immediately to locate the common roots of Eqs. (3.21), (3.22). Alternatively, some further transformations can be used to reduce the order of the polynomials to $N/2$. For maps this reduction is more complicated than the one we have applied for the ODE system. Since it is of no importance for the analysis of the ecological models discussed in this work, we omit the details of the calculations here. The application of resultants in map systems will be discussed in detail in (Gross and Feudel 2004a).

3.4 Advantages of resultants

Several methods for the computation of Hopf bifurcations have been discussed in this chapter. Generally speaking, we can distinguish three classes of methods: indirect methods, bordered matrix methods and classical methods.

The indirect methods are in a certain way the most straight forward approach. They can only be used for numerical computations, but have the advantage of high numerical stability.

In practice, bordered matrix methods are used more frequently. Although they are only locally convergent they have been shown to be more efficient than the indirect methods. This is in particular true if continuation of Hopf bifurcations is desired.

Classical methods exploit the symmetry of the imaginary eigenvalue pair. They are rarely used in numerical bifurcation analysis, although some methods based on classical approaches have been implemented. For analytical bifurcation analysis classical methods are in general advantageous since they do not generate unwanted information (e.g. additional eigenvalues, eigenvectors).

A historical point of view

Classical methods have been widely used for stability analysis before computers became available. However, the first numerical algorithms for the computation of Hopf bifurcations that were implemented on computers were mostly indirect methods. Later advances in computer hardware, programming languages and numerical analysis made the efficient implementation of bordered matrix methods possible. The availability of computers and bifurcation software stimulated a rapid development of dynamical systems theory. Because of the success of indirect and bordered matrix methods, the classical methods, which are more difficult to implement on computers have long been neglected. However, during the last years powerful computer algebra packages like Maple and Mathematica have become available. In the framework of computer algebra the classical methods can be implemented easily. For instance, the bialternate matrix product as well as Sylvester and Bezout resultants are included in

Maple's *LinearAlgebra* library. In the light of these new developments it is time to reconsider the classical methods.

Advantages of classical methods

Using classical methods testfunctions for the existence of center symmetric eigenvalues can be derived. In small and intermediate systems these testfunctions can often be solved analytically. This yields explicit expressions for bifurcation surfaces, which are otherwise difficult to obtain. If a testfunction can not be solved explicitly, its roots can be computed numerically. In Guckenheimer and Myers (1996) the numerical evaluation of testfunctions found by using Bezout resultants was found to be more efficient than the widely used bordered matrix method of Griewank and Reddien (1983). Another advantage of the classical methods is their analytical nature which is advantageous for the application in efficient continuation schemes, the calculation of normal form coefficients and the extension to bifurcations of higher codimension.

Comparison between resultants and the bialternate product

Among the classical methods the bialternate product has recently received much attention (Govaerts 2000). In comparison to the Sylvester resultant the bialternate product is easier to implement in numerical codes. Furthermore, the bialternate product method avoids the computation of coefficients of the characteristic polynomial, which is known to be numerically unstable. However, for our computer algebra based approach these numerical advantages are not of importance, since the implementation is easy and the coefficients are not calculated numerically, but analytically.

The main difficulty that has to be overcome in computer algebra based bifurcation analysis is the growing complexity of the solutions. Although the complexity of the final solution (e.g. the bifurcation surface) should not depend on the method, the complexity of intermediate solutions does vary. Here the Sylvester resultant has an advantage. The computation can be carried out in two steps: computation of the coefficients and computation of the resultant. For the Sylvester resultant both steps involve the computation of a determinant of size N or $N - 1$. That means, the complexity is balanced between the two steps. This is an advantage since simplifications and substitutions can be made after the first step. By contrast, the first step is simpler for the bialternate product method while the second is much more complex because of the large size of the determinant.

Another advantage of the Sylvester resultant is the simple structure of the determinant. In comparison the structure of the bialternate product matrix is much more complicated. The smaller size and simpler structure is advantageous for analytical proofs.

Finally, the fact that the Hopf number can be easily computed from subresultants is a great advantage. A similar procedure employing bialternate products has not been discovered so far.

Chapter 4

A model for general food chains

In this chapter we formulate the general food chain model on which the majority of our ecological conclusions are based. Instead of trying to describe a specific food chain we aim to gain general insights in the functioning of ecological systems as such. Despite its generality, the model can be analyzed with tools of local bifurcation theory. In this way the model enables us to study the local dynamics of ecological systems in a very general way. Although we present some results, the emphases of this chapter is on the formulation of the model. The advantages of the general approach will become apparent in the subsequent chapters. In Chap. 5 we apply the general model to formulate a possible solution for the famous paradox of enrichment. In Chap. 6 the general model is used to prove that chaotic dynamics generally occur in long food chains.

We motivate our general treatment of food chains with a brief review of specific food chain models in Sec. 4.1. The general model is formulated in Sec. 4.2. Most importantly the model is normalized in a way that enables us to compute the local bifurcations. In order to illustrate this analysis bifurcation diagrams for food chains of different length are computed in Sec. 4.3. The results of this chapter are summarized in Sec. 4.4.

4.1 Strength and weakness of specific models

The central task one faces in mathematical modeling is to describe the processes observed in nature in the language of mathematics. To this end most mathematical models employ specific functional forms. These functions are fitted to observations by tuning a number of parameters. However, because of the complexity of ecological systems every function that is proposed to model a given process can only be an approximation of reality. The conclusions that are drawn from a specific model are therefore based on an implicit assumption. We

have to assume that the behavior of the model does not depend strongly on the exact functional forms that are used in modeling. Otherwise the dynamics of the natural system may differ qualitatively from the dynamics of the model. In the present work we show that this danger is very real in models of ecological food chains.

A food chain is a simple trophic system in which the species are arranged into different levels. In a classical food chain every trophic level is occupied by a only one species. However, many food chain models are studied which describe more complex systems. In this case all species that populate the same trophic level are described by a single state variable. For instance the phytoplankton-zooplankton food chain proposed by Steele and Henderson (1992) consists of two state variables which denote the total abundances of phytoplankton and zooplankton respectively.

A food chain model has to describe the interactions of species among each other and with the environment. Examples of interactions with the environment are the uptake of nutrients or accidental death because. These interaction are modeled in the form of growth and mortality terms. Among each other the species in the food chain interact primarily by predation. This interaction is described in models by the so-called response functions.

In the past many different food chain models have been studied. The first model of ecological food chains was proposed independently by Lotka (1925) and Volterra (1926). By applying the law of mass action, known from chemistry, Lotka and Volterra derived a very simple mathematical description of predation. The simplicity of the model enabled Lotka and Volterra to obtain an analytical solution and to make testable predictions. However, in the early experiments by Gause (1934) it became apparent that the Lotka-Volterra model offers only a very rough description of nature.

Better models of food chains can be derived by taking additional biological details into account. For instance by considering that the predator needs a finite time for “handling” the prey after capture the so-called Monod function can be obtained. This function was proposed independently by Michaelis and Menten (1913) in the context of biochemistry, by Monod (1949) in the context of microbiology and by Holling (1959) in the context of entomology. The Monod function offers a better description of predation than the simpler function used in the Lotka-Volterra model. However, many aspects of the complex nature of predation are still not considered. By taking further biological details into account a large number of “realistic” models may be obtained. Among others the transition of prey to invulnerable states (Abrams and Walters 1996), interference of predators (DeAngelis et al. 1975) and the effect of hunger on the predator (Ivlev 1961) have been considered in literature.

In view of the large number of different mathematical descriptions of predation that may be derived experimental confirmation or rejection of specific response functions would be desirable. However, experimentally it is only possible to distinguish between broad classes of functions. For instance the dependence

of predation on prey abundance that can be observed in nature can be classified into three or four distinct types (Holling 1961). These Holling types, which will be discussed in more detail in Chap. 5, are classes of qualitatively different forms of predator-prey interaction. While it is in general possible to distinguish different Holling types in experiments (Verity 1991), it is extremely difficult to reject one of two functions of the same Holling type (Mullin et al. 1974).

Since direct experimental evidence that points toward a specific mathematical formulation of predation is in general not available it seems reasonable to use the simplest function that agrees with the experiments. Simple models are advantageous for analytical and numerical analysis. Furthermore, the available amount of experimental data is often not sufficient to fit the larger number of parameters found in more complex functions. Consequently, it is not surprising that the majority of ecological models considered today are still based on very simple mathematical functions.

Despite their advantages simple mathematical models should be treated with caution. Think of the implicit assumption which we have mentioned at the beginning of this section. Whenever we model a given interaction by a specific mathematical function we risk to end up with a system that does not describe the *generic* behavior observed in nature. In other words, we may have overlooked some aspect of biological reality that has an important impact on the model. Conclusions on the dynamics that are based on specific models may therefore have very limited range of validity. Even if the same behavior is predicted by several specific models, other models may exist which make radically different predictions. In fact, we show in Chap. 5 that the stability of steady states depends very sensitively on the shape of the response function. In Chap. 6 we show that certain degeneracies arise in models in which the mortality terms are exactly linear. Furthermore, we prove in Chap. 7 that competing predators can coexist in a stationary state if intraspecific competition between predators is taken into account. By contrast, such a coexistence is impossible in simpler models.

In order to avoid the degeneracies and uncertainties that arise in specific models we follow a different approach. In this chapter we formulate and analyze a general food chain model that does not rely on specific functional forms. In the subsequent chapters we apply this model to check whether results from specific models hold in the general context.

4.2 Formulation of a general food chain model

In the past the global stability and persistence of general models has been studied by Saunders and Bazin (1974), Gard (1980), Freedman and So (1985) and others. But, the investigation of local bifurcations has, to our knowledge, not been addressed in a general context. In this section we present an approach for the investigation of the local stability of steady states in a general food chain model.

4.2.1 The general model

Let us consider a simple, general food chain of N trophic levels. In a simple food chain there is exactly one *model species* on every trophic level. This model species represents either a single species or a group of similar species (e.g. say, phytoplankton). We number the model species from the primary producer (species 1) to the top-predator (species N). The size of the population of species n is denoted by the variable X_n . Depending on the system under consideration X_n can stand for abundance, biomass density or any other variable that quantifies the size of the population. In the following we use these terms equivalently.

The dynamics of the food chain can be described by a set of N ordinary differential equations. We assume that each species feeds only on the species on the immediately lower trophic level. The biomass loss of species n due to predation by species $n + 1$ is described by a general function $F_n(X_n, X_{n+1})$. We take into account that only a fraction η_{n+1} of the consumed prey biomass can be transformed into predator biomass.

Apart from predation other terms have to appear in the model. The primary producer grows by feeding on nutrients which are not modeled explicitly. We assume that the primary production can be described by a function $S(X_1)$. Primary producer mortality (apart from predation) can also be included in $S(X_1)$. The biomass loss of other species is modeled in form of mortality terms $M_n(X_n)$. These terms represent biomass loss due to natural death, maintenance costs, diseases or predation by predators which are not modeled explicitly. For the top predator we call the mortality term $D(X_N)$ (instead of $M_N(X_N)$) to indicate that it plays a different role in the dynamics of the model. Taking these factors into account we obtain the ODE system

$$\begin{aligned}\dot{X}_1 &= S(X_1) - F_1(X_1, X_2), \\ \dot{X}_n &= \eta_n F_{n-1}(X_{n-1}, X_n) - F_n(X_n, X_{n+1}) - M_n(X_n), \\ \dot{X}_N &= \eta_N F_{N-1}(X_{N-1}, X_N) - D(X_N),\end{aligned}\tag{4.1}$$

where n runs from 2 to $N - 1$.

4.2.2 Normalization of the model

So far we have formulated a general food chain model. Let us now study the stability of steady states in this model. In general, one would start this analysis by computing the abundances in the steady state. However, this is not possible with the chosen degree of generality. In fact, we can not even compute the number of steady states. We avoid this difficulty by assuming that a positive, but not necessarily stable, steady state X_1^*, \dots, X_N^* exists. We define normalized variables

$$x_n := \frac{X_n}{X_n^*} \quad \text{for } n = 1, \dots, N.\tag{4.2}$$

and normalized biomass flows

$$f_n(x_n, x_{n+1}) := \frac{F_n(X_n^* x_n, X_{n+1}^* x_{n+1})}{F_n(X_n^*, X_{n+1}^*)} \quad \text{for } n = 1, \dots, N-1 \quad (4.3)$$

$$s(x_1) := \frac{S(X_1^* x_1)}{S(X_1^*)}, \quad (4.4)$$

$$d(x_N) := \frac{D(X_N^* x_N)}{D(X_N^*)}. \quad (4.5)$$

The biomass can be normalized in this way since it is generally reasonable to assume that they do not vanish in the steady state. By contrast, we have to be more careful in the normalization of the mortality terms. We define

$$m_n(x_n) := \begin{cases} M_n(X_n^* x_n)/M_n(X_n^*) & \text{for } M_n(X_n^*) \neq 0 \\ 0 & \text{for } M_n(X) = 0 \text{ for all } X \end{cases} \quad (4.6)$$

This definition allows us to consider systems in which the mortality is neglected “by design”. In both cases we can use the normalized variables and flows to write Eq. (4.1) as

$$\begin{aligned} \dot{x}_1 X_1^* &= s(x_1)S(X_1^*) - f_1(x_1, x_2)F_1(X_1^*, X_2^*), \\ \dot{x}_n X_n^* &= \eta_n f_{n-1}(x_{n-1}, x_n)F_{n-1}(X_{n-1}^*, X_n^*) \\ &\quad - f_n(x_n, x_{n+1})F_n(X_n^*, X_{n+1}^*) - m_n(x_n)M_n(X_n^*), \\ \dot{x}_N X_N^* &= \eta_N f_{N-1}(x_{N-1}, x_N)F_{N-1}(X_{N-1}^*, X_N^*) \\ &\quad - d(x_N)D(X_N^*). \end{aligned} \quad (4.7)$$

for $n = 2, \dots, N-1$. Let us consider the system in the normalized steady state

$$x_1^* = \dots = x_N^* = 1. \quad (4.8)$$

By applying the definitions of the normalized biomass flows we find

$$f_n(x_n^*, x_{n+1}^*) = 1 \quad \text{for } n = 1, \dots, N-1 \quad (4.9)$$

$$s(x_1^*) = d(x_N^*) = 1, \quad (4.10)$$

and

$$m_n(x_n^*) = \begin{cases} 1 & \text{for } M_n(X_n^*) \neq 0 \\ 0 & \text{for } M_n(X) = 0 \text{ for all } X \end{cases} \quad (4.11)$$

By applying these relations to Eq. (4.7) we obtain

$$\frac{S(X_1^*)}{X_1^*} = \frac{F_1(X_1^*, X_2^*)}{X_1^*} =: \alpha_1 \quad (4.12)$$

$$\frac{\eta_n F_{n-1}(X_{n-1}^*, X_n^*)}{X_n^*} = \frac{F_n(X_n^*, X_{n+1}^*)}{X_n^*} + \frac{M_n(X_n^*)}{X_n^*} =: \alpha_n \quad (4.13)$$

$$\frac{\eta_N F_{N-1}(X_{N-1}^*, X_N^*)}{X_N^*} = \frac{D(X_N^*)}{X_N^*} =: \alpha_N. \quad (4.14)$$

Since only constants appear, these equations hold even if the system is not in the steady state.

In this work the parameters $\alpha_1, \dots, \alpha_N$ and other parameters defined below are called *general parameters*. We use this name to indicate, that these parameters describe general properties of ecological systems.

By applying the definition of α_1 to Eq. (4.7) we can simplify the differential equation of the primary producer to

$$\dot{x}_1 = \alpha_1 (s(x_1) - f_1(x_1, x_2)). \quad (4.15)$$

Likewise, applying the definition of α_N to the differential equation for the top-predator yields

$$\dot{x}_N = \alpha_N (f_{N-1}(x_{N-1}, x_N) - d(x_N)). \quad (4.16)$$

In order to simplify the other differential equations in a similar way we define additional general parameters

$$b_n := \frac{1}{\alpha_n} \frac{F_n(X_n^*, X_{n+1}^*)}{X_n^*}. \quad (4.17)$$

Comparing Eq. (4.17) to the second line of the definition of α_n reveals

$$1 - b_n = \frac{1}{\alpha_n} \frac{M_n(X_n^*)}{X_n^*}. \quad (4.18)$$

In terms of the parameters b_n and α_n we can write

$$\dot{x}_n = \alpha_n (f_{n-1}(x_{n-1}, x_n) - b_n f_n(x_n, x_{n+1}) - (1 - b_n)m_n(x_n)). \quad (4.19)$$

The normalization presented in this section is a crucial step in the analysis of the model. By means of the normalization we have managed to rewrite the model in such a way that the unknown steady state does not appear explicitly anymore. Although the general parameters depend in general on the unknown steady state we show in Sec. 4.2.4 that they can be interpreted biologically.

4.2.3 Stability of steady states

The previous section has shown that the normalized model can be written as

$$\begin{aligned} \dot{x}_1 &= \alpha_1 (s(x_1) - f_1(x_1, x_2)), \\ \dot{x}_n &= \alpha_n (f_{n-1}(x_{n-1}, x_n) - b_n f_n(x_n, x_{n+1}) - (1 - b_n)m_n(x_n)), \\ \dot{x}_N &= \alpha_N (f_{N-1}(x_{N-1}, x_N) - d(x_N)). \end{aligned} \quad (4.20)$$

Let us now return to the question of local asymptotic stability. The stability of the normalized steady state is in general determined by the Jacobian in the steady state. In our food chain model only certain terms appear in the Jacobian. We define the general parameters

$$\phi := \left. \frac{\partial s(x_1)}{\partial x_1} \right|_{\mathbf{x}=\mathbf{x}^*}, \quad (4.21)$$

$$p := \left. \frac{\partial d(x_N)}{\partial x_N} \right|_{\mathbf{x}=\mathbf{x}^*}. \quad (4.22)$$

$$\gamma_n := \left. \frac{\partial f_n(x_n, x_{n+1})}{\partial x_n} \right|_{\mathbf{x}=\mathbf{x}^*} \quad \text{for } n = 1, \dots, N-1 \quad (4.23)$$

$$\psi_n := \left. \frac{\partial f_n(x_n, x_{n+1})}{\partial x_{n+1}} \right|_{\mathbf{x}=\mathbf{x}^*} \quad \text{for } n = 1, \dots, N-1 \quad (4.24)$$

$$\mu_n := \left. \frac{\partial m_n(x_n)}{\partial x_n} \right|_{\mathbf{x}=\mathbf{x}^*} \quad \text{for } n = 2, \dots, N-1 \quad (4.25)$$

Using these parameters the Jacobian in the normalized steady state can be written as

$$\mathbf{J} = \begin{pmatrix} \alpha_1 & & & & & \\ & \alpha_2 & & & & \\ & & \ddots & & & \\ & & & \alpha_{N-1} & & \\ & & & & \alpha_N & \\ \begin{pmatrix} \phi - \gamma_1 & -\psi_1 & & & \\ \gamma_1 & (\psi_1 - \omega_2) & -b_2\psi_2 & & \\ & & \ddots & \ddots & \\ & & & \gamma_{N-2} & (\psi_{N-2} - \omega_{N-1}) & -b_{N-1}\psi_{N-1} \\ & & & & \gamma_{N-1} & (\psi_{N-1} - p) \end{pmatrix} \end{pmatrix}.$$

where vanishing elements have been omitted and $\omega_n := b_n\gamma_n + (1 - b_n)\mu_n$.

Note that we can write the Jacobian in a given steady state entirely in terms of the general parameters. The general parameters provide all the information that is required to compute the local bifurcations of the steady state under consideration. However, based on the Jacobian alone we can not distinguish between sub-critical and super-critical Hopf bifurcations or between generic saddle-node bifurcations and transcritical bifurcations since this would require additional information on the normal form coefficients. In order to include this information in the general model additional general parameters would have to be defined. Although this would certainly be rewarding it is beyond the scope of the present work.

4.2.4 Parameters and simplifications

So far we have used mathematics to rewrite and simplify the model. Most importantly, the unknown steady state does no longer appear explicitly in the model equations. This advantage has been gained by introducing a number of general parameters. Let us now study these parameters in more detail and consider further simplifications based on biological reasoning. The discussion presented here although outlines the range in which ecologically reasonable values of the parameters lie.

Timescales $\alpha_1, \dots, \alpha_N$ and relative timescale r

From the way in which the parameters $\alpha_1, \dots, \alpha_N$ appear in Eq. (4.20) it can be seen that they denote characteristic timescales of the species. One of these parameters, say α_1 can always be set to one by renormalizing the time coordinates. After the normalization the other parameters $\alpha_2, \dots, \alpha_N$ denote the relative length of the characteristic timescales.

In most food chains found in nature an allometric slowing down has been observed (Yodzis and Innes 1992, Hendriks 1999). That means, the ratio $r = \alpha_n/\alpha_{n+1}$ is independent of the trophic level n . We can model this universal relationship by assuming

$$\alpha_n = r^{n-1}. \quad (4.26)$$

In general the characteristic timescale of a predator will be longer than the timescale of its prey. In this work we consider the range $0 < r < 1$. In the singular perturbation limit $r = 0$ the timescales are completely separated. By contrast, $r = 1$ indicates that the characteristic timescales of predator and prey are identical.

Nutrient availability ϕ

The parameter ϕ is related to the supply of nutrients. According to Eq. (4.21) $\phi = 1$ means that the primary production is proportional to the abundance of the primary producer. This is typically the case if nutrients are abundant. However, if nutrients are scarce the primary production is not limited by the number of primary producers, but by the available nutrients. In an extreme case the primary production may remain unchanged if we increase the number of primary producers. This corresponds to $\phi = 0$.

Predator sensitivity $\gamma_1, \dots, \gamma_{N-1}, \Gamma$

The parameters $\gamma_1, \dots, \gamma_{N-1}$ describe the sensitivity of the predators on the availability of prey. If prey X_n is abundant the value of γ_n will in general approach zero. If prey is scarce the value of γ_n is larger. A typical case is $\gamma_n = 1$, which indicates that predation is proportional to the prey density. Interestingly, the value of γ_n depends strongly on the feeding strategy employed by the predator. This relationship is studied in detail in Chap. 5.

In the following we visualize our results in the form of bifurcation diagrams. In these diagrams we can only vary up to three parameters at a time. In order to reduce the number of parameters we assume

$$\gamma_1 = \dots = \gamma_{N-1} =: \Gamma. \quad (4.27)$$

The conclusions presented here do not depend on this assumption in a critical way. The bifurcation diagrams can look slightly different if the values of $\gamma_1, \dots, \gamma_{N-1}$ are changed independently. However, small variations in these parameters do not alter our results qualitatively. Only if $\gamma_1, \dots, \gamma_{N-1}$ are chosen very differently some new bifurcations can appear. This is illustrated in Chap. 6.

Predator interference $\psi_1, \dots, \psi_{N-1}$

The parameters $\psi_1, \dots, \psi_{N-1}$ describe the dependence of the predation on the predator abundance. In many food chains it is reasonable to assume that the individuals of a species of predators do not interfere. Consequently, the predation term is proportional to the numbers of predators and the corresponding parameter ψ_n is one. However, in other food chains intraspecific competition between predators can be observed. This is in general the case if other resources than prey are limiting.

Exponent of closure p

The most important mortality term in the model is the so-called closure term $d(x_N)$. The related parameter p is called the *exponent of closure*. The value of this parameter depends on the cause of the mortality. Let us, for instance assume, that mortality occurs mainly because of aging and natural death of individuals. In this case the mortality is roughly proportional to the biomass density and the exponent of closure is one (cf. Eq. 4.21). By contrast most diseases inflict a biomass loss which is proportional to the square of the population density. If such a disease is the main cause for top-predator mortality the exponent of closure is two. If multiple causes for mortality exist the exponent of closure is in general between one and two. The impact of the exponent of closure on the dynamics of the food chain is studied in Chap. 6.

Mortality exponents μ_2, \dots, μ_{N-1} **and branching ratios** b_2, \dots, b_{N-1}

The parameters μ_2, \dots, μ_{N-1} are very similar to the exponent of closure. These parameters likewise describe the dependence of the mortality of corresponding species on their biomass density. We will therefore call them mortality exponents. Unless noted otherwise we assume that these parameters are one. This choice corresponds to linear mortality terms.

The remaining parameters b_2, \dots, b_{N-1} will be called branching ratios. They characterize the branching of the biomass flow. The parameter b_n indicates the portion of the biomass loss of species n that occurs because of predation (cf. Eqs. (4.12), (4.13), (4.14), (4.17)). If the mortality $M_n(X_n)$ of species n is much larger than the predation biomass loss $F_n(X_n, X_{n+1})$ the parameter b_n is close to zero. By contrast $b_n = 1$ indicates that the loss of biomass occurs only because of predation.

In most of our investigations we neglect all mortality terms apart from the closure term and set $b_2 = \dots = b_{N-1} = 1$. We show in Chap. 6 that this assumption is not critical.

4.3 Bifurcations in general food chains

In this section we investigate the impact of the parameters r , Γ and ϕ on the dynamics of food chains. The main purpose of this analysis is to illustrate the general approach. However, we are able to draw some general conclusions which provide a basis for the subsequent chapters. In the following we focus on food

chains of length two to six. Longer food chains are extremely rare. The most attention will be devoted to food chains of length three or four since they are more frequent than longer food chains, but more interesting than food chains of just two levels.

Let us consider the local dynamics of simple food chains. For these first investigations we assume linear top predator mortality ($p = 1$), and absence of intraspecific competition in predator populations ($\psi_1 = \dots = \psi_{N-1} = 1$). Furthermore we set $\gamma_1 = \dots = \gamma_{N-1} = \Gamma$ and neglect the mortality of all species except the top predator ($b_2 = \dots = b_{N-1} = 1$). Finally, we assume that the timescales exhibit an allometric slowing-down $\alpha_n = r^{n-1}$.

Local bifurcations of the di-trophic food chain

For the purpose of illustration we start by considering the di-trophic (that is, two level) food chain. The Jacobian of this food chain can be written as

$$\mathbf{J} = \begin{pmatrix} 1 & 0 \\ 0 & r \end{pmatrix} \times \begin{pmatrix} (\phi - \Gamma) & -1 \\ \Gamma & 0 \end{pmatrix}. \quad (4.28)$$

From the Jacobian the general saddle-node and Hopf bifurcations of the normalized steady state can be computed. For the general saddle-node bifurcations we demand

$$0 = |\mathbf{J}| = r\Gamma, \quad (4.29)$$

which yields only the trivial solutions $r = 0$ and $\Gamma = 0$.

In two dimensional systems Hopf bifurcations can be found by explicit calculation of the eigenvalues. Let us nevertheless apply the method of resultants. By computing the resultant (cf. Eq. (3.12)) we obtain the condition

$$\Gamma = \phi \quad (4.30)$$

Computation of the Hopf number according to Eq. (3.16) yields

$$\chi = -r\Gamma. \quad (4.31)$$

Since the Hopf number is negative for $r > 0$ and $\phi > 0$, Eq. (4.30) describes a Hopf bifurcation surface. At $r = 0$ or $\phi = 0$ the Hopf bifurcation ends in a Takens-Bogdanov bifurcation.

A three-parameter bifurcation diagram for the di-trophic food chain is shown Fig. 4.1. Let us introduce this uncommon type of diagram by discussing Fig. 4.1 in detail.

The three parameter axes of the bifurcation diagram span a three dimensional space. Every point in this space corresponds to a class of specific systems with the respective values of Γ , r and ϕ . In the diagram the Hopf bifurcation appears as a red surface while the trivial surfaces that correspond to general saddle-node bifurcations are not shown. The Hopf bifurcation surface divides the space into two *volumes* in which the dynamics is qualitatively different. By

numerical computation of the eigenvalues of the Jacobian in one arbitrary point we can check that the normalized steady state is stable in the upper volume. If we start in the upper volume and vary the values of parameters the steady state remains stable until the Hopf bifurcation surface is crossed. In the entire lower volume the normalized steady state is unstable.

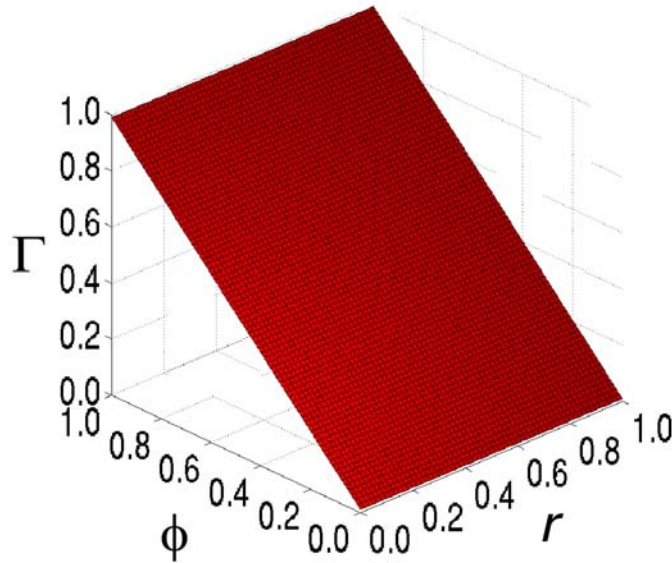


Figure 4.1: Bifurcation diagram of a general di-trophic food chain. The stability of the normalized steady state depends on the predators sensitivity to prey density Γ , the relative timescale of the predator dynamics r and the availability of nutrients ϕ . If parameters are changed a Hopf bifurcation (red surface) can be crossed. The steady state is stable above the Hopf bifurcation and unstable below.

Apart from the local bifurcations of steady states, local bifurcation of cycles as well as global bifurcations can exist. With the chosen degree of generality these bifurcations can not be computed or plotted in the diagram. In the case of the di-trophic food chain we can guess that a homoclinic bifurcation emerges from the Takens-Bogdanov bifurcation.

Local bifurcations of the tri-trophic food chain

In the literature many examples of tri-trophic (three level) food chains have been studied (Boer et al. 1998, De Feo and Rinaldi 1998, Edwards and Bees 2001). In the context of the general model the local bifurcations of general tri-trophic food chains can be computed. Like in case of the di-trophic chain we find trivial bifurcation surfaces at $r = 0$ and $\Gamma = 0$. Such surfaces exist in all ecological models considered here. In the following we will not mention these surfaces explicitly unless they play a role in the formation of higher codimension

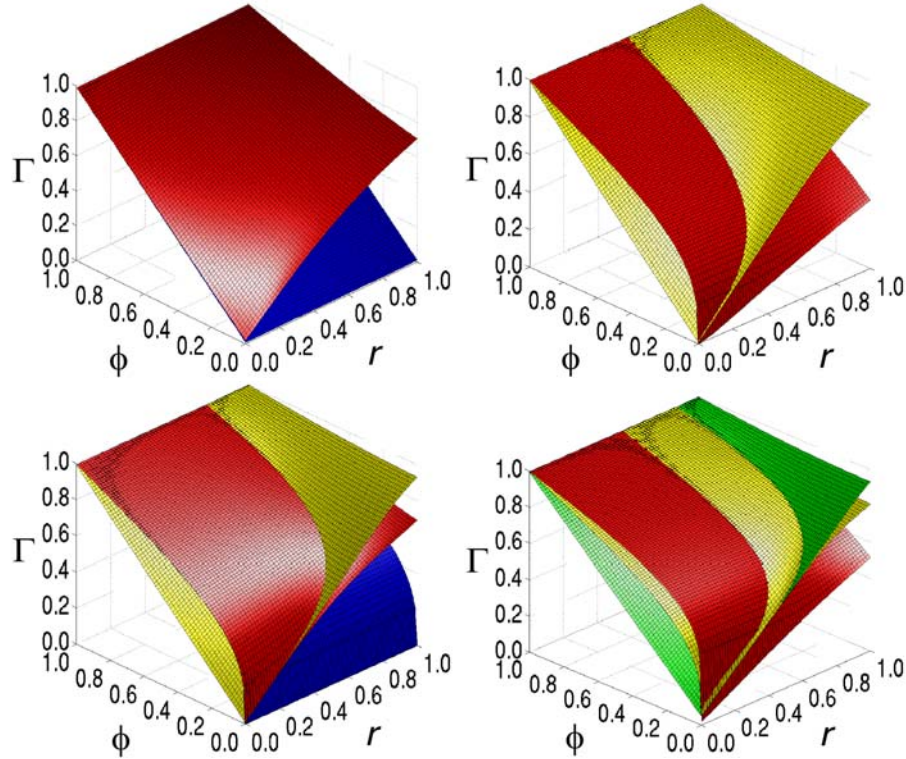


Figure 4.2: Local Bifurcations of tri-trophic (top left), four-trophic (top right), five-trophic (bottom left) and six trophic (bottom right) food chains respectively. The parameter space is spanned by predator sensitivity Γ , nutrient supply ϕ and timescale separation r . As the length of the chains is increased more Hopf bifurcation surfaces (red, green, yellow) appear. A general saddle-node bifurcation surface (blue) is only present for food chains of odd length.

bifurcations.

Apart from the trivial surfaces we find a non-trivial surface of Hopf bifurcations and a non-trivial surface of general saddle-node bifurcations. The bifurcation surfaces are shown in the top-left diagram of Fig. 4.2. In this work general saddle-node bifurcation surfaces are always shown in blue. All other colors correspond to surfaces of Hopf bifurcations.

The two bifurcation surfaces shown in the diagram divide the parameter space into three volumes. In this diagram and all following ones, the normalized steady state is always stable in the top-most volume of parameter space and unstable everywhere else. The normalized steady state of the tri-trophic food chain is therefore stable above the Hopf bifurcation and unstable below.

Like in the di-trophic case local bifurcations of higher codimension are only formed at the boundary of the parameter space shown. The Hopf bifurcation

surface ends in a Takens-Bogdanov bifurcation at $(\phi = 1, \Gamma = 1)$ and in a degenerate Takens-Bogdanov-like bifurcation of codimension-3 at $(r = 0, \Gamma = \phi)$. Although a detailed analysis of these degenerate bifurcations has not been carried out their presence indicates that a homoclinic bifurcation is likely to exist.

Local bifurcations of four-, five- and six-trophic food chains

A bifurcation diagram of a general four-trophic food chain is shown as the top-right diagram of Fig. 4.2. In this food chain we have two non-trivial bifurcation surfaces that correspond to Hopf bifurcations. At the intersection of the two Hopf bifurcation surfaces a codimension-2 double Hopf bifurcation line is formed.

In the bifurcation diagram of the general five-trophic food chain (bottom-left in Fig. 4.2) we find two Hopf bifurcation surfaces and a general saddle-node bifurcation surface. Again, a line of double Hopf bifurcations is formed at the intersection of the two Hopf bifurcation surfaces. In addition a line of Gavrilov-Guckenheimer bifurcations exists at the intersection of the yellow Hopf bifurcation surface with the general saddle-node bifurcation surface (blue). This bifurcation line lies below the red Hopf bifurcation surface and is therefore not visible in the diagram.

The bottom-right diagram of Fig. 4.2 shows a bifurcation diagram for general six trophic food chains. In the six-trophic case three Hopf bifurcation surfaces exist. Double Hopf bifurcations are formed on three lines in which two of the bifurcation surfaces intersect. Of these double Hopf bifurcation lines two are visible in the diagram. The third double Hopf bifurcation line is formed at the intersection of the red and the green bifurcation surface and is located below the yellow bifurcation surface.

Note, that the formation of double Hopf bifurcations indicates that chaotic parameter regions generally exist in the food chains under consideration. This result holds independently of the functional form of the interactions.

Local bifurcations in longer food chains

Food chains of more than six trophic levels are very rare in nature. Nevertheless it is instructive to formulate some general insights that hold independently of food chain length. We show in Chap. 7 that many of these insights also apply to food webs of similar complexity.

In our brief discussion we have already noted that the normalized steady state is always stable in the top-most volume of parameter space. In other words, this means that high values of Γ have a stabilizing effect on steady states. If the parameter Γ is decreased below a critical value bifurcations occur in which the steady state becomes unstable. In the examples considered so far this primary loss of stability occurs always in a Hopf bifurcation. However, as we will see in Chap. 7 a destabilization in a general saddle-node bifurcation is also possible. Under the assumptions made above a general saddle-node bifurcation is present in all food chains of odd length. The number of Hopf bifurcation

surfaces that exist in food chains of length N is in general $N/2$ (rounded down). In addition trivial bifurcation surfaces exist at $r = 0$ and $\Gamma = 0$.

Bifurcations of higher codimension are formed by the interaction of Hopf bifurcation surfaces among themselves or with general saddle-node bifurcation surfaces. In short food chains ($N \leq 3$) local bifurcations of higher codimension only occur at the boundary of the considered parameter space. The trivial bifurcation surfaces on which they are formed are likely to be degenerate. Nevertheless, the fact that the Hopf bifurcation ends at these surfaces suggests that another bifurcation in which a limit cycle vanishes is in general present.

In longer food chains ($N > 3$) local non-trivial bifurcations of codimension-2 are formed. In the examples considered so far we have observed Gavrilov-Guckenheimer and double Hopf bifurcations. However, Takens-Bogdanov bifurcations can also occur if other parameters are varied. For our investigations in Chap. 6 the double Hopf bifurcations are particularly important. Note that these bifurcations exist in all food chains of four or more trophic levels.

4.4 Summary

In this chapter a general food chain model has been proposed. In the formulation of this model we have avoided to restrict the ecological processes to specific functional forms. Instead, the process were described by general functions which were not specified. Despite the generality of the model we were able to compute local bifurcation diagrams. The primary purpose of these investigations was to prove that such an analysis can be performed in the first place. Nevertheless, we have already made two important observations.

Our investigations have revealed that the effect of the predator-prey interaction on the stability can be measured in terms of the parameter Γ . The bifurcation diagrams show that high values of Γ always have a stabilizing effect on the food chain. This insight is used in the next chapter to study the effect of enrichment on the stability.

Furthermore we have seen that double Hopf bifurcations appear in all food chains of four or more trophic levels. This proves that chaotic parameter regions generically exist in long food chains. We discuss this result in more detail in Chap. 6.

Chapter 5

The Paradox of Enrichment

In this chapter we study the famous paradox of enrichment. This paradox revolves around the destabilization of ecological systems as a response to an increased supply of nutrients. In our discussion of the paradox we follow the approach outlined in the previous chapter. The applications of the general model reveals that the paradox of enrichment may be caused by assumptions that are regularly made in specific models. In this way our treatment of the paradox of enrichment serves as an illustration and motivation for the general approach.

We start with a brief review of the paradox of enrichment in Sec. 5.1. Thereafter the general model is applied in Sec. 5.2. We identify the sensitivity to prey density as a key parameter for the stability of the enriched system. In Sec. 5.3 this parameter is computed for a number of specific response functions. Our analysis reveals that enrichment has always a destabilizing effect on these functions. However, in Sec. 5.4 we propose a realistic function which behaves in a qualitatively different way. A sufficient condition that indicates this alternative behavior in response functions is derived in Sec. 5.5. Finally in Sec. 5.6, we discuss the implications of our result in the context of ecological modeling.

5.1 The classical paradox of enrichment

Many ecological systems provide important resources. It is therefore often tried to increase the amount of these resources that can be harvested from a given system. Intuitively one would think, that this can be achieved by *enriching* the system, that is by increasing the amount of available nutrients. Although this is in many cases successful, it was noted by Huffaker et al. (1963) that enrichment can destabilize ecological systems. In a systematic study Rosenzweig (1971) showed that the destabilizing effect of enrichment can be observed in many ecological models. Generally, increasing the amount of available nutrients increases the average abundance of species, but at the same time destabilizes steady states

(Rosenzweig 1977, 1995, May 1987, Gilpin 1972, Abrams and Roth 1994). While the species should in principle be able to survive in a non-stationary state, it is often observed that oscillations grow rapidly until extinction occurs (Cunningham and Nisbet 1983, Pascual and Caswell 1997).

Rosenzweig called the observed behavior “Paradox of Enrichment” to indicate that a beneficial influence (enrichment) can have a detrimental and therefore paradoxical effect (extinction). However, from a dynamical point of view this situation is not too paradoxical. Increasing the amount of nutrients relaxes the nutrient limitation of the primary producer and increases the amount of prey available to predators. As a result a Hopf bifurcation occurs. If this bifurcation is supercritical stable oscillations may be observed for some time. But as the system is enriched further subsequent bifurcations can occur. In fact, we have shown in Chap. 4 that a homoclinic bifurcation is likely. Therefore we can expect that stable oscillations can only be observed in a very limited parameter interval.

While the dynamics of Rosenzweig’s paradox have been well understood another question has become apparent. Over the years there have been only very few successful attempts to demonstrate the paradox of enrichment in experiments (Luckinbill 1974, Tilman and Wedin 1991, Morin and Lawler 1995). In other cases enrichment did not destabilize the system (McAllister et al. 1972, McCauley and Murdoch 1990) or had a stabilizing effect (Kirk 1998).

In order to explain the disagreement between theory and experiment several modifications of the simple models have been proposed. For instance the existence of invulnerable individuals in the prey population (Abrams and Walters 1996), self-limitation of predator growth (DeAngelis et al. 1975, Kirk 1998), nonlinear mortality of the predator (Bazykin 1974) and spatial heterogeneity (Jansen 1995) have been considered.

We propose a different solution to the paradox of enrichment. In this chapter we study how the destabilizing effect of enrichment arises in simple ecological models and show how this source of instability can be avoided.

5.2 Effects of Enrichment

Let us consider the effects of enrichment in the context of our general food chain model. Since enrichment increases the abundance of species it effects most of the general parameters at least slightly. Destabilization occurs if the parameters change in such a way that a Hopf bifurcation surface is crossed. In Sec. 5.1 we have identified the nutrient availability ϕ and the predator’s sensitivity to prey $\gamma_1, \dots, \gamma_{N-1}$ (or Γ) as key parameters for the paradox of enrichment. In Chap. 6 we show that the effect of enrichment on other parameters is in general weakly

stabilizing. Since our primary aim is to understand the cause of instability we do not consider the impact of enrichment on these parameters here.

In the following we focus on the sensitivity parameters $\gamma_1, \dots, \gamma_{N-1}$. Essentially the same analysis can be applied for the nutrient availability ϕ . However, by studying the sensitivity parameters additional insights on the impact of predator response functions can be gained.

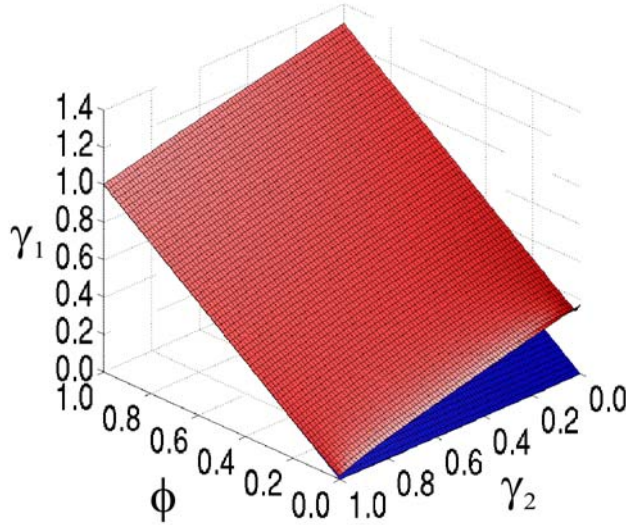


Figure 5.1: Bifurcation diagram of a tri-trophic food chain. The parameter γ_1 denotes the sensitivity of the first predator to the abundance of the primary producer while γ_2 is the sensitivity of the top predator to the first predator. The parameter ϕ denotes the availability of nutrients. The normalized steady state is stable above the Hopf bifurcation (red surface) and unstable below. The blue surface corresponds to a general saddle-node bifurcation. Enrichment can destabilize the food chain by increasing ϕ or decreasing γ_1 or γ_2 .

In the previous chapter we have assumed that the sensitivity of predation to prey abundance is similar on all levels of the food chain. That is, $\gamma_1 = \dots = \gamma_{N-1} = \Gamma$. The analysis presented in that chapter confirmed that increasing Γ has a stabilizing effect on general food chains. This result does in general extend to the individual parameters $\gamma_1, \dots, \gamma_{N-1}$. Consider for instance the bifurcation diagrams of the tri-trophic food chain shown in Fig. 5.1. The sensitivity of the two predators to the abundance of their prey in the chain is described by parameters γ_1 and γ_2 . These parameters and the availability of nutrients ϕ span a three dimensional parameter space. The normalized steady state is stable in the top-most volume of the parameter space and unstable everywhere else. The diagram shows that the steady state of the tri-trophic food chain can be stabilized

by increasing γ_1 . Likewise, increasing γ_2 has a stabilizing effect since it decreases the critical value of γ_1 at which the Hopf bifurcation (red surface) occurs.

Although small regions exist in which other behavior is observed we can say that an effect which increases one of the parameters $\gamma_1, \dots, \gamma_{N-1}$ is generally stabilizing. On the other hand an effect which decreases one of these parameters is generally destabilizing.

5.3 Specific response functions

In order to determine whether enrichment is stabilizing or destabilizing the food chain we have to ask whether it is increasing or decreasing the value of the parameters $\gamma_1, \dots, \gamma_{N-1}$.

In many ecological models it is assumed that the function $F_n(X_n, X_{n+1})$ can be separated into a prey dependent part $G_n(X_n)$ and a predator dependent part $E_n(X_{n+1})$ so that

$$F_n(X_n, X_{n+1}) = G_n(X_n)E_n(X_{n+1}) \quad (5.1)$$

The function $G_n(X_n)$ is called *predator functional response* or *predator response function*. By applying Eqs. (4.21 - 4.25) we obtain

$$\gamma_n = \frac{\partial}{\partial x_n} \frac{F_n(X_n^* x_n, X_{n+1}^* x_{n+1})}{F_n(X_n^*, X_{n+1}^*)} \Big|_{x_n=1} = \frac{X_n^*}{G_n(X_n^*)} \frac{\partial}{\partial X_n} G_n(X_n) \Big|_{X_n=X_n^*}. \quad (5.2)$$

In the past several different response functions have been proposed. In this section we discuss several commonly used response functions and compute the corresponding values of γ_n . In these computations we drop the index n for the sake of simplicity.

According to the classification of Holling (1959) the first type of predator responses observed in nature are linear functions. The most simple response function that is commonly used in ecological literature is the Lotka-Volterra response

$$G_{LV}(X) = AX, \quad (5.3)$$

where A is a constant factor. We apply Eq. (5.2) and obtain

$$\gamma_{LV} = 1. \quad (5.4)$$

If the Lotka-Volterra function is used in a given model enrichment has no effect on the corresponding parameters γ . However, the Lotka-Volterra model assumes that the amount of prey that is consumed by a single predator is proportional to the prey density. This assumption is reasonable if prey is scarce, but it is clearly unrealistic for high prey densities. The Lotka-Volterra function is therefore not

well suited to describe the effects of enrichment. In order to avoid this problem the rectilinear response

$$G_{\text{RL}}(X) = \begin{cases} AX & \text{for } X \leq K \\ AK & \text{for } X > K \end{cases} \quad (5.5)$$

has been proposed. In this function the predator becomes saturated when the prey density exceeds a certain level K . We can write the corresponding prey sensitivity γ_{RL} as a function of the dimensionless parameter

$$\chi = \frac{X^*}{K}. \quad (5.6)$$

This yields

$$\gamma_{\text{RL}}(\chi) = \begin{cases} 1 & \text{for } \chi < 1 \\ 0 & \text{for } \chi > 1 \end{cases} \quad (5.7)$$

In this function a very strong form of the paradox of enrichment appears. As soon as the prey density reaches the saturation threshold the sensitivity drops discontinuously from 1 (very stable) to 0 (very unstable).

One could argue that the sudden destabilization of the rectilinear response is only caused by its piecewise definition. A more realistic description of predator saturation is offered by the response functions of Holling type II. These functions are described as curvilinear responses by Holling. They start out linearly, but smoothly approach some saturation value as the density of prey increases. The most prominent Holling type II response is the Monod function

$$G_{\text{HD}}(X) = \frac{AX}{K + X}, \quad (5.8)$$

which is also known as Michaelis-Menten equation (Michaelis and Menten 1913) or Holling's disk¹ equation (Holling 1959). The Monod function is a very prominent function that is used in a large number of ecological models. Nevertheless other response functions of Holling type II have been proposed. An example is the function

$$G_{\text{IV}}(X) = A(1 - \exp(-X/K)), \quad (5.9)$$

which has been derived by Ivlev (1961). Although the $G_{\text{IV}}(X)$ and $G_{\text{HD}}(X)$ are different the graphs of the two functions are very similar (cf. Tab. 5.1). Likewise the corresponding sensitivity function

$$\gamma_{\text{HD}}(\chi) = \frac{1}{1 + \chi}, \quad (5.10)$$

$$\gamma_{\text{IV}}(\chi) = \frac{\chi}{\exp(\chi) - 1} \quad (5.11)$$

¹ In some of Holling's experiments the predators were blindfolded students which hunted for sandpaper *disks* in an otherwise empty room.

behave in a similar way. For vanishing prey density the sensitivity is one. As the prey density is increased the sensitivity decreases monotonously. In the limit of high prey density the sensitivity approaches zero for both functions. This proves that enrichment has always a destabilizing effect on these functions.

It has often been remarked that type III response functions are in general more stable than the functions of type II. Let us therefore investigate the effect of enrichment on these functions. The most common type III function is

$$G_{\text{H3}}(X) = \frac{AX^2}{K^2 + X^2}. \quad (5.12)$$

This function is sometimes called vertebrate functional response, since it was proposed by Holling to describe vertebrates. However, it has been shown that it describes the behavior of many invertebrates as well (Hassel 1978). In contrast to the Holling type II functions type III functions have a sigmoid shape. Sigmoid response are observed if predators become less effective if prey densities are low. Alternatively, it has been argued that the success probability for attacks can suffer from a lack of practice at low prey densities. The corresponding sensitivity function

$$\gamma_{\text{H3}}(\chi) = \frac{2}{1 + \chi^2} \quad (5.13)$$

is two for vanishing prey density and therefore very stable. However, the sensitivity decreases monotonously with increasing prey density. At high prey densities $\gamma_{\text{H3}}(\chi)$ even drops below $\gamma_{\text{HD}}(\chi)$. This shows that enrichment has a strong destabilizing effect if sigmoid responses are used in a given model.

Another function that is sometimes used to describe sigmoid predator response is the multiple saturation function

$$G_{\text{MS}}(X) = \prod_{m=1}^M \frac{AX}{X + K_m}. \quad (5.14)$$

This response function is a product of M Monod functions. Because of the derivative in Eq. (5.2) the corresponding sensitivity function

$$\gamma_{\text{MS}}(\chi_1, \dots, \chi_M) = \sum_{m=1}^M \frac{1}{1 + \chi_m} \quad (5.15)$$

is a sum of the Monod sensitivities. Although the sensitivity of the multiple saturation function is always higher than that of the individual Monod functions it cannot escape the destabilizing effect of enrichment. As prey density is increased the sensitivity decreases monotonously and approaches zero for high prey densities.

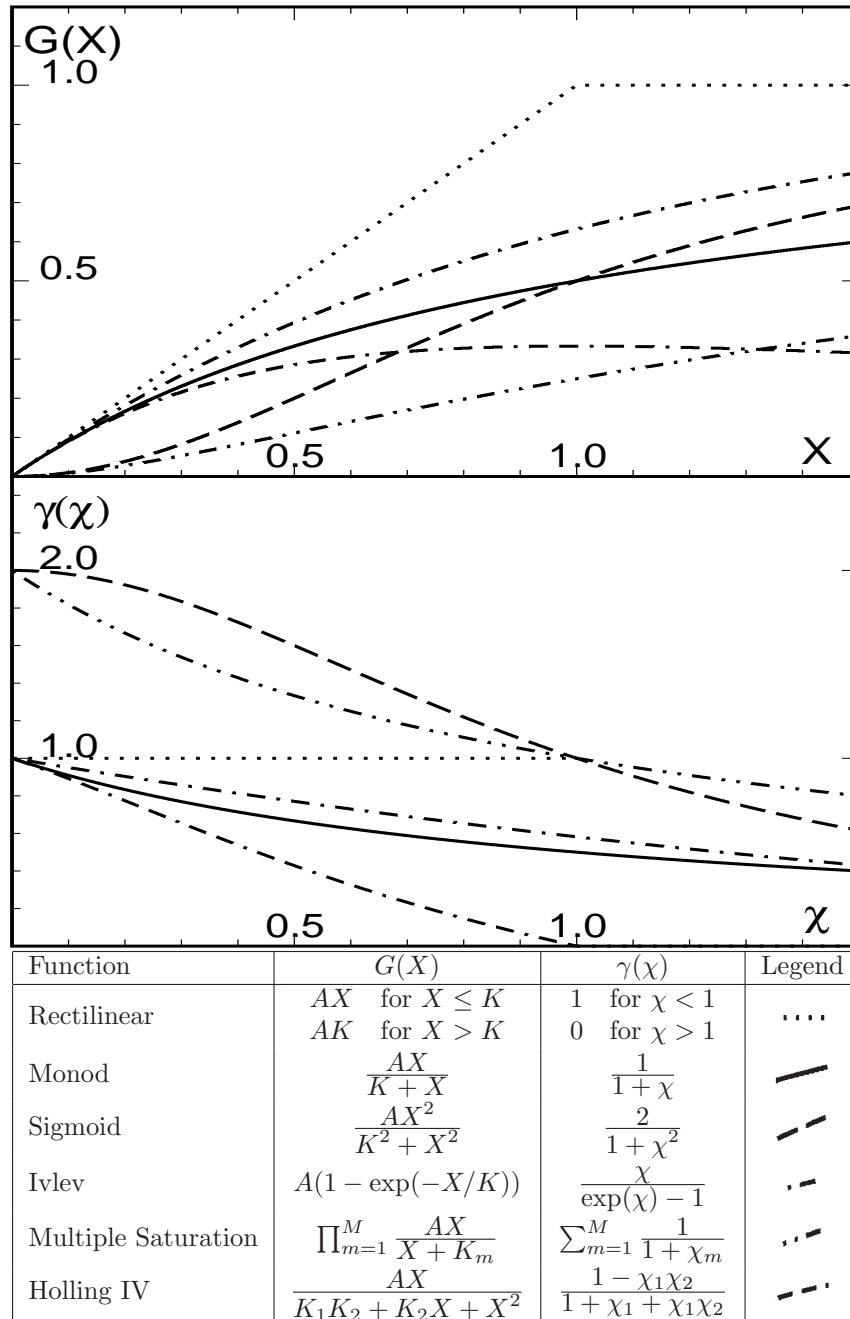


Table 5.1: The common response functions $G(X)$ correspond to monotonously decreasing stability functions $\gamma(\chi)$, where $\chi = X^*/K$ and $\chi_m = X^*/K_m$. The plots show the functions for $A = 1$, $M = 2$ and $K = K_1 = K_2 = 1$.

Let us finally consider an example in which the sensitivity does not vanish in the limit of high prey density. Consider for instance the so-called Holling type IV function

$$G_{\text{H4}}(X) = \frac{AX}{K_1K_2 + K_2X + X^2} \quad (5.16)$$

In contrast to the response functions discussed so far this function describes a system in which exceedingly high prey density is detrimental for the predator. At low prey densities the functional response increases with increasing prey density. However, at a certain density a maximum is reached. If the prey density is increased further the functional response decreases again. Such behavior can occur if the prey employs some collective defense against the predator. The corresponding sensitivity function

$$\gamma_{\text{H4}}(\chi_1, \chi_2) = \frac{1 - \chi_1\chi_2}{1 + \chi_1 + \chi_1\chi_2} \quad (5.17)$$

depends on two parameters $\chi_1 = X^*/K_1$ and $\chi_2 = X^*/K_2$. For very low prey densities the sensitivity is close to one. As the prey abundance is increased the sensitivity function decreases monotonously. As the response function reaches the maximum the sensitivity becomes zero. At higher prey densities the sensitivity is negative. This means that the predators will consume less prey if more prey is available. Food chains with group defense in the prey population are therefore in general rapidly destabilized by enrichment.

Apart from the Lotka-Volterra response all response functions we have considered so far behave in a qualitatively similar way. The corresponding sensitivity functions decrease monotonously with increasing prey density. We can identify this destabilizing effect as a major cause of the paradox of enrichment. In the light of these findings it is not surprising that ecological models based on these functions are generally destabilized by enrichment. However, the fact that all prominent response functions behave in a certain way does not imply that the same has to be true for all other response functions.

5.4 A solution to the paradox

Let us now ask whether a response function exists on which enrichment has a stabilizing effect. We have to consider that $\gamma(\chi)$ depends on the slope of $G(X)$. Consequently, $\gamma(\chi)$ has to vanish if $G(X)$ approaches some non-zero saturation value. Since realistic response functions should in general take predator saturation into account the paradox of enrichment seems to be inevitable. Once the prey concentration is so high that the predator is saturated its sensitivity to prey abundance has to approach zero. However, this does not imply that the stability has to decrease monotonously. As the abundance of prey is increased the system may pass through several maxima and minima of stability.

Let us for example consider an imaginary species of predators. These predators hunt by employing either one of two strategies. We assume that the first

strategy can be described by a Holling type II response function

$$G_{S1}(X) = \frac{AX}{K + X}. \quad (5.18)$$

while the second strategy follows a Holling type III response

$$G_{S2}(X) = \frac{AX^2}{K^2 + X^2}. \quad (5.19)$$

We can now write the effective response function $G_{\text{Eff}}(X)$ as a weighted sum of $G_{S1}(X)$ and $G_{S2}(X)$. Assuming that the predators are more likely to employ the more advantageous strategy we choose $G_{S1}(X)/G_{S2}(X)$ as the weight for the first strategy and $G_{S2}(X)/G_{S1}(X)$ as the weight for the second strategy. This yields

$$G_{\text{Eff}}(X) = \frac{\frac{G_{S1}(X)}{G_{S2}(X)}G_{S1}(X) + \frac{G_{S2}(X)}{G_{S1}(X)}G_{S2}(X)}{\frac{G_{S1}(X)}{G_{S2}(X)} + \frac{G_{S2}(X)}{G_{S1}(X)}} \quad (5.20)$$

Compared to the response functions discussed so far $G_{\text{Eff}}(X)$ is relatively complex. Nevertheless it still describes biologically simple behavior. The upper diagram in Fig. 5.2 shows a comparison between $G_{\text{Eff}}(X)$ and $G_{S1}(X)$. At low prey densities strategy one is clearly advantageous. Almost all predators are therefore employing strategy one and $G_{\text{Eff}}(X)$ is nearly identical to $G_{S1}(X)$. But as the prey density is increased some predators start to employ strategy two. Since this is still a disadvantage the function $G_{\text{Eff}}(X)$ drops a little bit below $G_{S1}(X)$. However, as the abundance of prey is increased further, strategy two becomes more advantageous and $G_{\text{Eff}}(X)$ rises a little above $G_{S1}(X)$. Despite these minor differences the two response functions shown in the diagram look very similar. To distinguish these functions in an experiment would be extremely difficult.

Let us compute the sensitivity function that corresponds to Eq. (5.20). Application of Eq. (5.2) yields

$$\gamma_{\text{Eff}}(\chi) = \frac{1+5\chi^2-2\chi^3+24\chi^4+22\chi^5+66\chi^6+78\chi^7+93\chi^8+58\chi^9+33\chi^{10}+4\chi^{11}+2\chi^{12}}{(2\chi^2+\chi+1)(\chi^4+\chi^3+2\chi^2-\chi+1)(2\chi^4+2\chi^3+3\chi^2+1)(\chi+1)(\chi^2+1)} \quad (5.21)$$

This function has been plotted in the lower diagram of Fig. 5.2. A comparison with the sensitivity $\gamma_{S1}(\chi)$ that corresponds to strategy one reveals the following: At low prey densities the functions are very similar. But, as some predators start to employ strategy two $\gamma_{\text{Eff}}(\chi)$ falls below the sensitivity of $\gamma_{S1}(\chi)$. It is interesting to note that in this region $G_{\text{Eff}}(X)$ is less stable than both strategy one and strategy two. However, as the prey density is increased further $\gamma_{\text{Eff}}(\chi)$ starts to increase again while $\gamma_{S1}(\chi)$ continues to decrease monotonously.

The example shows that the sensitivity depends strongly on the functional form of the predator-prey interaction. Although the two functions $G_{\text{Eff}}(X)$ and

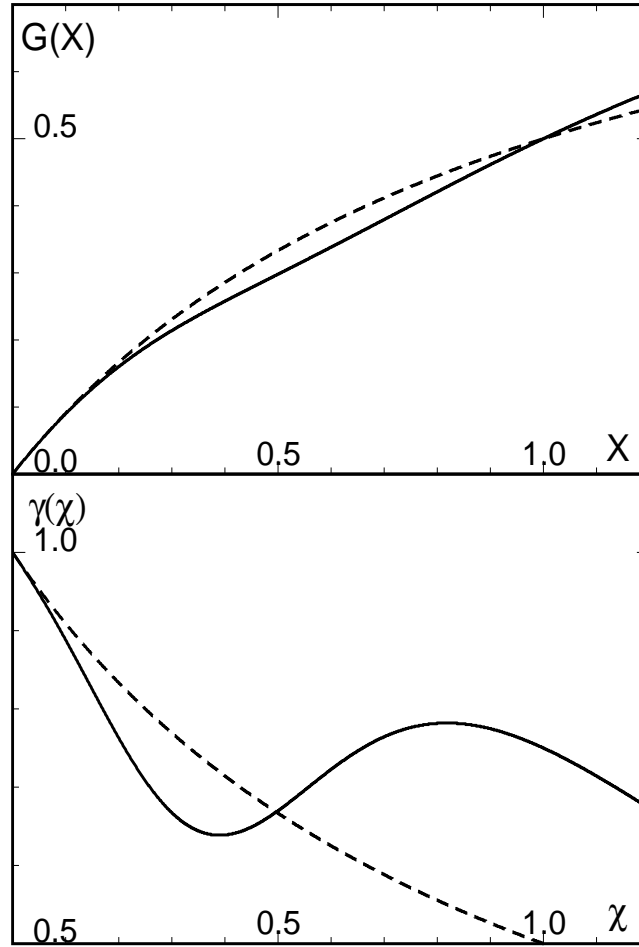


Figure 5.2: Comparison between the Monod function (dashed line) and the more complex functional response proposed in Eq. (5.20) (continuous line). Both response functions look very similar (upper diagram). However, they correspond to qualitatively different sensitivity functions (lower diagram). For the Monod function enrichment is always destabilizing since it decreases the sensitivity. By contrast, a large interval exists in which enrichment increases the stability of the more complex response.

$G_{S1}(X)$ look very similar the corresponding functions $\gamma_{\text{EFF}}(\chi)$ and $\gamma_{S1}(\chi)$ are qualitatively different. Enrichment can not have a stabilizing effect on the simple response functions considered in Sec. 5.3. However, for the more complex response function proposed in Eq. (5.20) a large interval exists in which en-

richment increases the sensitivity and is therefore stabilizing. This shows that possible solutions to the paradox of enrichment can be found if more biological details are considered in the derivation of the response functions.

5.5 A condition for non-monotonic stability

So far we have only shown that a response function can be constructed for which enrichment can have a stabilizing effect. As a next step it is reasonable to ask if this response function is only a single pathological example or a representative of a large class of functions. We answer this question by deriving a sufficient condition which indicates an increasing sensitivity in a certain parameter range.

We define

$$S(X^*) := \left. \frac{\partial}{\partial X} G(X) \right|_{X=X^*}, \quad (5.22)$$

$$R(X^*) := \frac{G(X^*)}{X^*}, \quad (5.23)$$

which allows us to write Eq. (5.2) as

$$\gamma(X^*) := \frac{S(X^*)}{R(X^*)}. \quad (5.24)$$

Note that $S(X^*)$ is the slope of $G(X)$ in X^* while $R(X^*)$ is the average slope of $G(X)$ between zero and X^* .

Let us now consider the diagram in Fig. 5.3. The diagram shows the graph of $G_{\text{Eff}}(X)$. Furthermore, a line has been drawn in the diagram that touches the $G_{\text{Eff}}(X)$ in two points which we call X_1 and X_2 . The existence of such a common tangent proves that the slope of $G_{\text{Eff}}(X)$ is identical in the two points. In other words this means

$$S(X_1) = S(X_2). \quad (5.25)$$

At the same time the fact that the common tangent intersects the positive y-axis proves that the average slope in the left point X_1 is larger than in the right point X_2 and therefore

$$R(X_1) > R(X_2). \quad (5.26)$$

Assuming $R(X_2) > 0$ and $S(X_1) = S(X_2) > 0$ we obtain

$$\gamma(X_1) = \frac{S(X_1)}{R(X_1)} < \frac{S(X_1)}{R(X_2)} = \gamma(X_2), \quad (5.27)$$

This proves that the sensitivity increases in average between X_1 and X_2 . We can say, that the existence of the common tangent intersecting the positive y-axis implies that enrichment can have stabilizing effect on the response function.

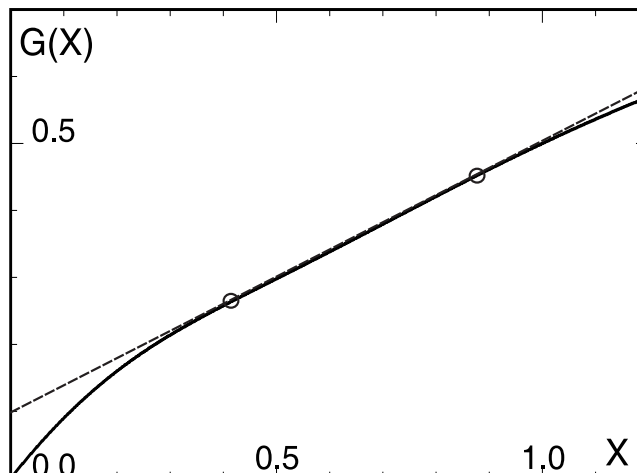


Figure 5.3: An illustration of the common tangent criterion. The dashed line in the diagram touches the graph of the response function Eq. (5.20) in two points (circled) and intersects the positive y-axis. The fact that such a common tangent exists proves that the stability of the response increases between the two points.

Although the common-tangent condition is only a sufficient condition it proves that enrichment has a stabilizing effect on a large class of response functions. Besides the switching of feeding strategies discussed above, one can think of many other forms of adaptation to prey density (Abrams and Roth 1994, Hassel 1978). Details of the predator-prey interaction may alter the response function only slightly but they can have a strong impact on the sensitivity of the response and therefore on the stability of the system.

5.6 The problem in the paradox

In this chapter we have proposed a solution for the paradox of enrichment. We have shown that the sensitivity of predator-prey interactions depends strongly on the shape of the response function. As a result biological details of predator-prey interaction can have a significant impact on the stability of the system. The commonly used response functions take only few biological details into account and model them with very simple mathematical functions. For these functions the sensitivity decreases monotonously as the prey density is increased. Therefore enrichment has a destabilizing effect on systems in which these functions are used. By contrast, more complex functions which take additional biological details into account are likely to have an increasing sensitivity in certain parameter ranges. These functions can therefore explain the stabilizing effect of enrichment that has been observed in experiments.

Our results show that minor changes in the response function can alter its sensitivity. Consequently, predators can escape the paradox of enrichment by adapting to prey density in certain ways. Since the paradox of enrichment is very disadvantageous from an evolutionary point of view it would not be surprising to find that the feeding behavior of many species has been optimized for stability as well as for predation rate. In this light it appears only natural that the paradox of enrichment has only rarely been observed in nature.

While the arguments presented above provide a solution to the paradox of enrichment they give rise to a deeper, more profound problem. The paradox of enrichment shows that the simple commonly used interaction functions may not predict the stability of steady states correctly. Of course, simplicity is desirable in models as long as it is consistent with experimental measurements. Simple response functions are widely used since no direct empirical evidence is available that would allow to reject these functions. However, the fact that natural systems are often *not* destabilized by enrichment, provides this evidence in an indirect way.

The experimental verification of response function is in general based on the measurement of abundances. Since the abundance of species is not very sensitive to the shape of the response function simple functions are sufficient to predict steady state abundances with good accuracy. By contrast, the stability of the system can depend strongly on the response. In this light it seems advisable to verify response functions by measuring the stability of a system under consideration as it has been done in the experiments by Fussmann et al. (2000).

From the theoretical point of view it would be highly desirable to derive criteria which allow the researcher to decide which types of effects can possibly have an impact on the stability of the system under consideration and should therefore be considered in models. Such criteria may be based on insights gained in the investigation of general models.

In the context of this work the results on the paradox of enrichment serve as a motivation as well as an illustration of the general approach. In this chapter many results have been obtained by considering specific interaction functions. However, our analysis as such was based on a result of the general model: the fact that the impact of the predator-prey interaction on the stability can be measured in terms of γ . The identification of general parameters has enabled us to compare different functions that are used in specific models. This was possible since we did not make any assumptions on the response functions in the general model.

Our results demonstrate that qualitatively different types of behavior may be possible despite the fact that a large number of specific models behave in

a similar way. These findings underline the need to verify conclusions from specific models in a general context.

Chapter 6

Chaos in general food chains

The previous chapter has shown that specific models may behave in a certain way while other realistic models exhibit a different kind of behavior. A very interesting and much debated question is whether chaos exists in nature. While chaos is found in some models it seems to be absent from others. In this chapter we use our general food chain model to investigate whether chaotic regions exist *generically* in long food chains. In particular we focus on the question whether stabilizing influences like strong, nonlinear mortality may prevent the formation of chaotic regions. In Chap. 7 we show that these results can be extended to a large class of food webs.

We start with a brief review of experimental and theoretical evidence for chaos in ecological systems. The computation of Lyapunov exponents - a numerical technique for the detection of chaotic dynamics - is introduced in Sec. 6.2. Our conclusions on the existence of chaos in general models are based on the computation of double Hopf bifurcations. However, we use the computation of Lyapunov exponents to illustrate our results in a specific example. These investigations are presented in Sec. 6.3. Finally, we summarize the results in Sec. 6.4.

In effect this chapter follows the lines of the (Gross et al. 2004). However, some additional material is presented in the second half of the chapter. In particular we show two examples for degenerate double Hopf bifurcations.

6.1 Chaos in ecology

In the investigation of chaos, examples from ecology have always played an important role. For instance May (1974, 1976) showed that very simple ecological

models can exhibit chaotic dynamics. While these examples have inspired many advances in dynamical systems theory the question whether chaos exists in nature is still debated (May 1987, Upadhyay et al. 1998, Rai and Schaffer 2001, Cushing et al. 2002).

In experiments chaos is generally difficult to detect because of the presence of observational noise (Nychka et al. 1992, Ellner and Turchin 1995). Nevertheless, chaos has been found for instance in the dynamics of perennial grasses (Tilman and Wedin 1991), flour beetles (Cushing et al. 1996) and boreal rodents (Hanski et al. 1993). Many other systems seem to be in critical states at the edge of chaos (Turchin and Ellner 2000).

From the theoretical point of view population dynamics should be chaotic if chaos is in principle possible in a given system and proves to be advantageous in the evolutionary context. Regarding the effect of chaos on the evolutionary fitness of species two main lines of reasoning exist. On the one hand it is argued that the seemingly random behavior that characterizes chaos can eventually cause the extinction of species Lande (1993). On the other hand, it has been proved that chaotic fluctuations are desirable in a spatially extended environment (Solé and Gamarra 1998, Petrovskii et al. 2004, Allen et al. 1993). Such fluctuations increase the chance that populations survive periods of detrimental conditions in isolated patches. Starting from these patches the surrounding area can be repopulated once the conditions improve. By contrast, a population with stationary or periodical dynamics is more likely to go extinct in the whole region. Following this line of reasoning chaotic dynamics can increase the chances of species survival. Consequently, it is reasonable to expect that ecological systems could evolve towards chaotic regions in parameter space if such regions exist.

While chaotic attractors have been found in many models (Hastings and Powell 1991, Boer et al. 1998) they seem to be absent from others (Steele and Henderson 1992, Ruxton and Rohani 1998). In particular it has been argued that chaotic regions may not exist in many ecological systems because of the strong damping effect of mortality on the dynamics. For instance it has been claimed by Steele and Henderson (1992) that quadratic mortality of the top predator prevents chaotic, quasiperiodic and even periodic dynamics in a plankton model. Although this was proved to be wrong by Edwards and Yool (2000) the question whether chaos exists generally in ecological systems remains open. It was shown by Ruxton and Rohani (1998) that chaotic regions exist in certain models, but disappear if the model structure is perturbed in a certain way. In fact, it has often been postulated that chaos would disappear if sufficient biological detail would be taken into account (Fussmann and Heber 2002, Kondoh 2003). However, from a dynamical systems point of view one would expect that increasing the complexity of the model is likely to increase the complexity of the dynamics as well (May 1973).

In a certain sense the question for the existence of chaos in nature is very similar to our investigation of the paradox of enrichment. In both cases the question is whether results from specific models describe the *generic* situation found in nature. In the following we use the general approach to show that chaotic parameter regions generically exist in long food chains. This result remains valid regardless of the functional form of the interactions. In particular we show that chaotic regions exist even if strong nonlinear mortality is considered in the model. Only in degenerate systems like Lotka-Volterra food chains the formation of chaotic regions can be avoided.

6.2 Detection of chaos in models

On a chaotic attractor the phase-space distance between trajectories with nearly identical initial conditions increases exponentially for a certain time. This divergence of neighboring trajectories is one of the main characteristics of chaos. We can measure the rate of divergence by computing the corresponding Lyapunov exponents (Guckenheimer and Holmes 2002 and others). For a given attractor in an N -dimensional system N Lyapunov exponents exist. These exponents describe the growth of small perturbations along the stable and unstable directions. Negative Lyapunov exponents indicate that small perturbations disappear in time. Positive Lyapunov exponents correspond to exponential growth of small perturbations.

If the system is in an asymptotically stable steady state all Lyapunov exponents are negative. On all other attractors found in systems of ODEs at least one Lyapunov exponent is zero. The zero Lyapunov exponent has to exist since the distance between two points on the same trajectory can in average neither increase nor decrease. For instance on a stable limit cycle the Lyapunov exponent that corresponds to perturbations in the direction of the cycle is zero; all other Lyapunov exponents are negative. They indicate that neighboring trajectories approach the cycle. On a two-torus two zero Lyapunov exponents which correspond to the two dimensional surface of the torus exist. Likewise, the dynamics on a three torus is characterized by three zero Lyapunov exponents. Chaotic dynamics can be observed on attractors on which at least one Lyapunov exponent is positive.

We can determine the dynamics on a given attractor by counting the number of negative, positive and zero Lyapunov exponents. In a specific system the numerical computation of Lyapunov exponents is in principle always possible. However, in practice the numerical convergence may be very slow. Despite the difficulties that can arise, the computation of Lyapunov exponents is frequently used. In Sec. 6.3.4 we apply this technique to investigate the dynamics of a specific model.

In our general model Lyapunov exponents can not be computed numerically. Although we have been able to compute the Jacobian in the normalized steady state the Jacobian on other attractors can not be obtained in the same way. Generally speaking, the attempt to find the chaotic attractor *directly* in the general model faces a principal difficulty. Our general food chain model has been constructed in such a way that it accommodates all the information that is necessary to determine the dynamics in the neighborhood of the normalized steady state. However, the model does not contain sufficient information on the global dynamics to investigate whether a chaotic attractor might exist elsewhere. However, it is possible to prove the existence of chaotic dynamics in the general model *indirectly*. In the indirect approach we deduce the existence of chaos from local bifurcations of higher codimension. In Chap. 2 we have argued that chaotic dynamics has to exist close to a double Hopf bifurcation. Thus, their existence can be considered as a strong indicator of chaos in food chain models.

In our three-parameter bifurcation diagrams the double Hopf bifurcations occur on lines consisting entirely of such bifurcation points. Since chaotic dynamics generically exist close to every single bifurcation point the chaotic parameter region extends along the double Hopf bifurcation line.

6.3 Chaos in food chains with mortality

The bifurcation diagrams shown in Chap. 4 (cf. Fig. 4.2) have revealed that double Hopf bifurcations exist in general food chains of four or more trophic levels. Therefore chaos generically exists in these food chains. In the bifurcation diagrams we have assumed that the mortality of the top predator is linear and that the biomass loss of the other species arises only because of predation. Let us now investigate whether the chaotic regions survive if additional nonlinear mortality terms are taken into account.

6.3.1 Causes of mortality

In this work we use the term mortality to denote any form of biomass loss except predation by explicitly modeled predators. The effect of mortality on model behavior depends in general on the functional form of the mortality terms. Let us therefore start our discussion of mortality by considering some specific mortality terms.

In many ecological populations mortality arises because of natural aging and death of individuals. Since this *natural mortality* effects every individual separately the total loss rate is proportional to the size of the population. We can write the corresponding mortality term as

$$M_n(X_n) = AX_n, \tag{6.1}$$

where A is a constant. The same reasoning can be applied to other causes of mortality as well. For example, in a dangerous environment the number of accidental death can be assumed to be proportional to the abundance of a species. In certain models the state variables denote not the abundance or density of species but the energy available to them (DeAngelis 1992). In this case linear loss terms are often used to model maintenance costs. These losses can be treated as linear mortality terms although they are not directly related to the death of individuals.

The reasoning which leads to the linear mortality terms is based on the law of mass action. This law states that the effect of a process that involves only one individual should be proportional to the total number of individuals. However, not every cause of mortality effects individuals separately. For instance the transmission of a disease has to involve at least two individuals. Consequently, most diseases inflict a biomass loss that is roughly proportional to the square of the population density. This corresponds to a mortality term of the form

$$M_n(X_n) = AX_n^2. \quad (6.2)$$

An interesting situation arises if a mortality term is used to model the effect of predators that are *not* part of the food chain. To model predators in this way is reasonable if their abundance can be assumed to be constant or at least independent of the state variables. This is in general true for predators that feed on many different species. The effect of such predators on the food chain depends on their feeding strategy. For instance Edwards and Bees (2001) show that predation by marine filtration feeders can be modeled by a linear mortality term while a quadratic mortality term is more appropriate for ambush feeders. In other ecological models the effect of implicitly modeled predators is described by more complex functions. For instance Ludwig et al. (1978) model the effect of predation on spruce budworm populations by

$$M_n(X_n) = \frac{AX^2}{K^2 + X^2} \quad (6.3)$$

where A and K are constant parameters.

The derivation of mortality terms that relate to predation is very similar to the derivation of response functions. In particular it faces the same difficulties and uncertainties that we have discussed in the context of the paradox of enrichment. However, even for mortality terms that do not correspond to predation similar uncertainties exist. For instance natural mortality is not entirely independent of other processes like predation. Although a linear mortality term may describe natural mortality very accurately we have to keep in mind that it is nevertheless only an approximation. It has been shown by Edwards and Bees (2001) that linear mortality terms describe a degenerate situation. In this case any small deviation from linearity may cause the transition to qualitatively

different dynamics. These insights demonstrate that it is desirable to investigate the impact of mortality in general models that are not based on specific functional forms.

6.3.2 Mortality in the general model

In the general food chain model mortality appears in the form of the general mortality terms $M_2(X_2), \dots, M_{N-1}(X_{N-1})$ and the closure term $D(X_N)$. Our investigations in Chap. 4 revealed that the impact of these functions on the stability of steady state can be measured in terms of the branching ratios b_2, \dots, b_{N-1} and the mortality exponents $\mu_2, \dots, \mu_{N-1}, p$. The branching ratios describe the relative strength of the mortality while the mortality exponents relate to the nonlinearity of the corresponding mortality term.

Let us compute the general parameters for some specific functional forms. Linear and quadratic mortality can be studied simultaneously by considering the monomial mortality term

$$M(X) = AX^z \quad (6.4)$$

with a constant exponent z . In this equation the index n has been dropped for the sake of simplicity. By applying Eq. (4.6) we obtain the normalized mortality term

$$m(x) = x^z. \quad (6.5)$$

In the normalization the constant A has vanished. This is reasonable since A determines only the magnitude of the mortality. It therefore effects b but not μ . According to Eq. (4.25) we compute the mortality exponent

$$\mu = \left. \frac{\partial}{\partial x} m(x) \right|_{\mathbf{x}=\mathbf{x}^*} = z. \quad (6.6)$$

For monomial mortalities the mortality exponent is identical to the exponent of the corresponding mortality term. Likewise, the exponent of closure p is the exponent of the closure term $D(X_N)$.

Mortality exponents that correspond to more involved mortality terms can be computed in the same way. This yields in general mortality exponents between one and two. Lower or higher mortality exponents only occur in special situations. For instance lower mortality exponents can occur if species are protected by laws that allow the harvesting of a fixed amount of biomass per year.

Among the mortality exponents the exponent of closure p has received the most attention in ecological literature (Edwards and Bees 2001). Unlike the other mortality exponents the exponent of closure describes the only cause of biomass loss for the top-predator. The mortality terms of the other species “compete” with the biomass losses that occur because of predation. Since predation is in many food chains more important than mortality the impact of the mortality exponents μ_2, \dots, μ_{N-1} is relatively weak. However the impact of the exponent of closure can be quite strong.

The effect of the exponent of closure on the dynamics is particularly interesting since the exponent of closure may depend strongly on the environment. For instance it has been shown by Rothschild and Osborn (1988) that the mortality of zooplankton is very sensitive to the turbulence of the surrounding water. Ambush feeders that feed on the top predator of a nutrient-phytoplankton-zooplankton food chain become less efficient as the turbulence is increased. At the same time the efficiency of filtration feeders and the number of accidental deaths caused by strong shear forces increases. Accidental death and predation by predation feeders correspond to an exponent of closure of one while predation by ambush feeders corresponds to an exponent of closure of two. The effective exponent of closure is therefore low (≈ 1) if the turbulence is high and high (≈ 2) if the turbulence is low. In this way the exponent of closure provides an important link between physics and biology.

6.3.3 Chaos in general food chains

The effect of the exponent of closure on the local bifurcations is shown in Fig. 6.1. The figure consists of four bifurcation diagrams that correspond to food chains of three, four, five and six trophic levels. In the diagrams the relative length of timescales r , the predator's sensitivity to prey density Γ and the exponent of closure p have been varied. The availability of nutrients ϕ has been set to 0.5. This value corresponds to a moderate nutrient level. Furthermore, we have assumed that the predators do not interfere ($\psi_2 = \dots = \psi_{N-1} = 1$) and that predation is the only cause of biomass loss for all species except the top-predator ($b_2 = \dots = b_{N-1} = 1$).

The surfaces in the diagram correspond to general saddle-node bifurcation surfaces (blue) and Hopf bifurcation surfaces (red, green, yellow). These bifurcations divide the parameter space into volumes of qualitatively different local dynamics. The normalized steady state is stable in the top-most volume of the bifurcation diagram and unstable everywhere else.

In Chap. 4 we have computed similar diagrams for food chains with linear closure (cf. Fig. 4.2). In that chapter we have observed that $N/2$ Hopf bifurcation surfaces exist in general N -trophic food chains. Figure 6.1 shows that these Hopf bifurcations extend to nonlinear closure.

In addition to the Hopf bifurcation surfaces a general saddle-node bifurcation surface is present in all diagrams. The bifurcation surface enters the positive parameter cone exactly at $p = 1$. This behavior provides further evidence for the degeneracy of food chains with linear closure, which has been noted by (Edwards and Bees 2001). In food chains of odd length the general saddle-node surface extends to high exponents of closure and leaves the diagram at $p = 2$. However, in food chains of even length the surface folds back towards low exponents of closure and leaves the diagram at $p = 1$. The different shape of the bifurcation

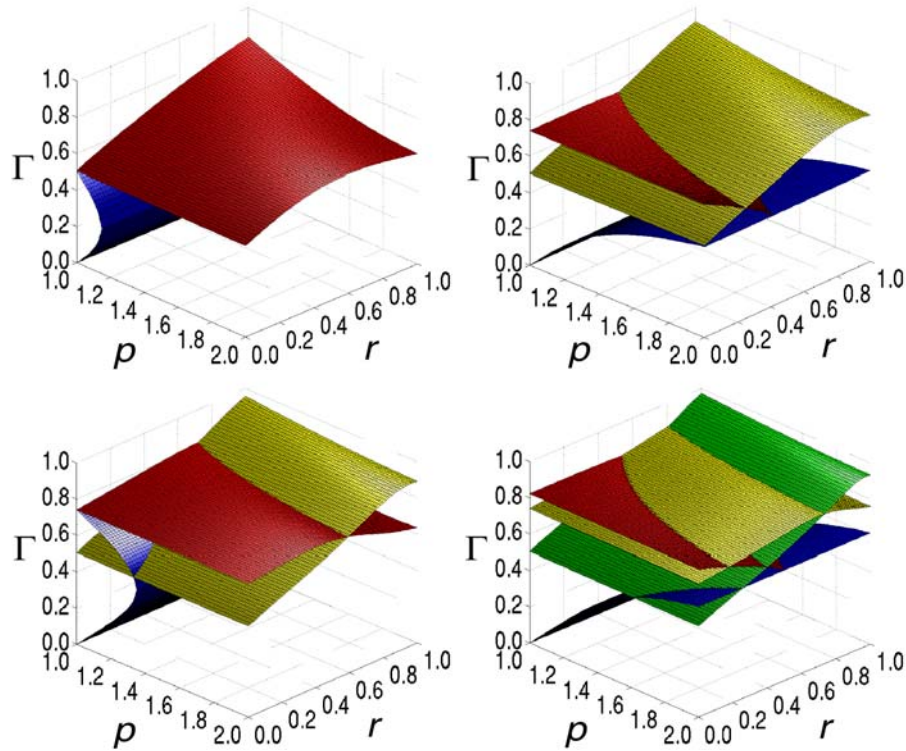


Figure 6.1: Bifurcation diagrams of food chains of length three (top left), four (top right), five (bottom left), six (bottom right). The dynamics around the steady state depends on the predator's sensitivity to prey density Γ , the exponent of closure p and the relative length of prey timescales r . The surfaces correspond to general saddle-node bifurcations (blue) and Hopf bifurcations (red, yellow, green). Local codimension-2 bifurcations are formed on the lines in which the codimension-1 bifurcation surfaces meet or intersect each other. Chaotic dynamics does in general occur near the double Hopf bifurcation lines that are formed at the intersection of two Hopf bifurcation surfaces.

surfaces explains the apparent absence of general saddle-node bifurcations in food chains of even length which we have observed in Fig. 4.2.

Bifurcations of codimension two are located on the lines in which the codimension-1 surfaces meet or intersect. A line of Takens-Bogdanov bifurcations is formed in the food chains of even length as the red Hopf bifurcation surface ends on the general saddle-node bifurcation surface. In the food chains of length five and six a line of Gavrilov-Guckenheimer bifurcations is located at the intersection of the green bifurcation surface and the general saddle-node bifurcation. Double Hopf bifurcations are formed at the intersection of two Hopf bifurcation

surfaces. In the four-trophic and five-trophic food chains a line of double Hopf bifurcations is located at the intersection of the red and green Hopf bifurcation surfaces. In the six-trophic food chain three double Hopf bifurcation lines are formed by the pairwise intersection of the three Hopf bifurcation surfaces. In longer food chains even more Hopf bifurcation surfaces exist. Consequently, we can expect that more double Hopf bifurcation lines are formed.

The presence of double Hopf bifurcations proves that chaotic parameter regions generically exist in food chains of four or more trophic levels. Moreover, the double Hopf bifurcation lines extend to high exponents of closure. This proves that high exponents of closure can not prevent chaos in long food chains.

The existence of chaos is the central result around which this chapter revolves. Nevertheless, some further observations regarding the stability of steady states can be made. We consider the critical value of Γ at which the top-most Hopf bifurcation is encountered for given values of r and p . The bifurcation diagrams show that the critical value of Γ decreases as the exponent of closure is increased. This shows that high exponents of closure have a stabilizing effect on the normalized steady state, although they will not generally prevent chaos.

Our analysis suggest that it is misleading to assume that parameter variations that have a stabilizing effect on steady states should also prevent chaos. Consider for instance the effect of r on the food chain. Intuitively one could think that a large separation of timescales should stabilize the system. However, the bifurcation diagrams show that this is not the case. The highest stability is often found at intermediate values of r . Let us for example consider the bifurcation diagram of the four-trophic food chain at a fixed value of p . The “most stable” choice of r is found in the point at which the double Hopf bifurcation occurs. At this value of r the critical Γ at which the destabilization occurs has the lowest possible value. However, once this critical value is crossed the dynamics become almost immediately chaotic since we are passing directly through the double Hopf bifurcation.

6.3.4 A specific example

So far we have shown that chaotic parameter regions generally exist in long food chains. Let us now consider a specific example in order to illustrate the emergence of chaos from the double Hopf bifurcation.

We consider a four-trophic food chain and assume logistic growth of the primary producer. The predator-prey interaction is assumed to be of Monod type. Furthermore we assume that predators do not interfere and that all mortality terms except the closure term can be neglected. This yields the ODE system

$$\dot{X}_1 = A_0(C - X_1)X_1 - \frac{A_1X_1X_2}{K_1 + X_1}, \quad (6.7)$$

$$\dot{X}_2 = \frac{B_1 X_1 X_2}{K_1 + X_1} - \frac{A_2 X_2 X_3}{K_2 + X_2}, \quad (6.8)$$

$$\dot{X}_3 = \frac{B_2 X_2 X_3}{K_2 + X_2} - \frac{A_3 X_3 X_4}{K_3 + X_3}, \quad (6.9)$$

$$\dot{X}_4 = \frac{B_3 X_3 X_4}{K_3 + X_3} - M X_4^p, \quad (6.10)$$

where $A_0, A_1, A_2, A_3, B_1, B_2, B_3, C, K_1, K_2, K_3$ and M are constant parameters. In the investigation of food chains observed one would normally choose the values of these parameters based on experimental measurements or theoretical reasoning. However, in this chapter our aim is to illustrate our general results in an arbitrary model. It is therefore reasonable to choose the parameters in such a way that the comparison to the general model becomes as simple as possible. We set

$$A_0 = 1/(C - 1), \quad (6.11)$$

$$A_n = r^{n-1}(K_n + 1) \quad \text{for } n = 1 \dots 3, \quad (6.12)$$

$$B_n = r^n(K_n + 1) \quad \text{for } n = 1 \dots 3, \quad (6.13)$$

$$M = r^3, \quad (6.14)$$

$$K_1 = K_2 = K_3 = K. \quad (6.15)$$

For this choice of parameters $X_1^* = \dots = X_4^* = 1$ is a steady state. This saves us the effort of the normalization. The parameter r and p denote the relative timescale separation and the exponent of closure as in the general model. We consider $r = 0.3$, which is realistic for many food chains observed in nature (Hendriks 1999). Furthermore, we assume $C = 3$ which corresponds to $\phi = 0.5$ in the general model. The relationship between the half saturation parameter K and the predator sensitivity Γ can be written as

$$\Gamma = \frac{K}{K + 1}. \quad (6.16)$$

In this equation we have used the results on the Monod function from Sec. 5.3.

A comparison of results from the general and the specific model is shown in Fig. 6.2. The upper diagram in the figure shows local bifurcations that have been computed analytically in the general model. In the two parameter diagram the Hopf bifurcation surfaces appear as bifurcation lines. At the intersection of the two lines a double Hopf bifurcation point is formed. The existence of a chaotic region close to the double Hopf bifurcation is illustrated in the lower diagram. This diagram has been obtained by the numerical computation of Lyapunov exponents in the specific model (Shimada and Nagashima 1979).

The quasiperiodic route to chaos can be observed in the left part of Fig. 6.2. The dynamics is stationary for high values of Γ . At the Hopf bifurcation line a stable limit cycle emerges. In the white region shown in the diagram the dynamics is periodic. At lower values of Γ the attractor evolves first into a two

torus (medium grey region) and then a three-torus (light grey region). Finally the three-torus decays and a chaotic attractor is formed (black region).

Right of the double Hopf bifurcation the transition to chaos is much faster. We observe chaotic dynamics almost immediately after the Hopf bifurcation in which the steady state becomes unstable. It is possible that the chaotic region extends a little bit above the Hopf bifurcation. In this case the chaotic attractor would coexist with the steady state in some part of the region that is marked as stationary. We can not determine the nature of the transition to chaos with certainty. However, simulations in this region suggest the Shil'nikov route to chaos.

From the biological point of view the almost direct transition from stationary to chaotic dynamics is interesting. It has been shown by Petrovskii et al. (2004) that the formation of an chaotic attractor can prevent the large oscillations that are usually observed in enriched ecological models. In this way the transition to chaos can reduce the risk of extinction. In our example large oscillations are encountered at lower values of Γ . In this region phase lockings appear and the dynamics becomes periodic. In the minimum of these oscillations the abundance of the primary producer drops about 10 orders of magnitude below the equilibrium value. Extinction is therefore very likely in this region. In comparison, very low abundances are less pronounced and less frequent on the chaotic attractor.

Very close to the double Hopf bifurcation and for high exponents of closure regions exist in which all Lyapunov exponents are very small (dark grey). In these regions the numerical computation of the Lyapunov exponents converges very slowly. We can not determine the dynamics in this region with certainty. In this region the distance between neighboring trajectories will either increase or decrease very slowly. The existence of this region may explain why many systems observed in nature appear to be at the edge of chaos.

6.3.5 Additional mortality terms

The investigation of the general model and the specific example have revealed that chaotic parameter regions generally exist at high exponents of closure. However, in these investigations we have assumed that all other mortality terms can be neglected. Let us now study the impact of these additional mortality terms on food chains.

Let us consider a four trophic food chain with quadratic closure ($p = 2$). We study the case in which all other mortality terms are linear ($\mu_2 = \mu_3 = 1$). The strength of the additional mortality terms is determined by the parameters b_2 and b_3 . These parameters denote the portion of the total biomass loss that occurs because of predation. For the sake of simplicity we assume

$$b_2 = b_3 := B. \quad (6.17)$$

The bifurcation diagram for the four-trophic food chain shown in Fig. 6.1 corresponds to $B = 1$. In this case the entire biomass loss of species two and three

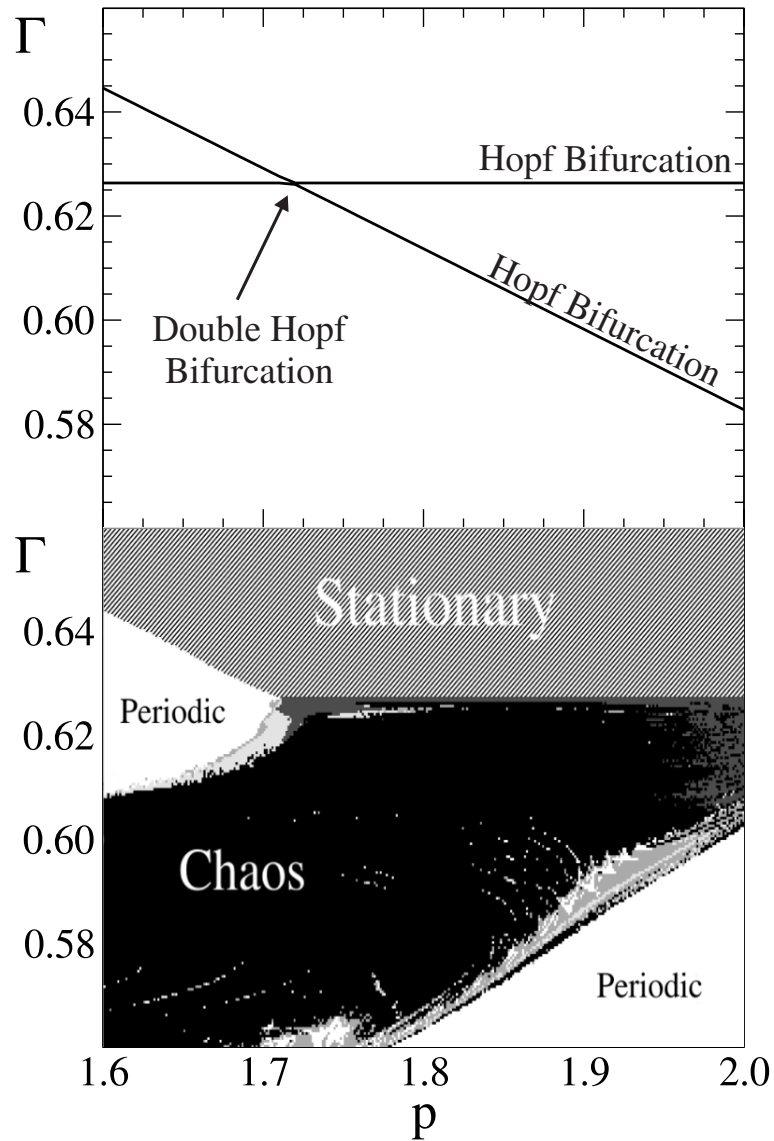


Figure 6.2: Comparison between results from the general and specific models. The axes of both diagrams are spanned by the predator's sensitivity to prey Γ and the exponent of closure p . Top: Local bifurcations in the general model. We find two lines of Hopf bifurcations which intersect in a double Hopf bifurcation point. Bottom: Dynamics in a specific model. Depending on the values of the parameters the attractor is a steady state (hatched), limit cycle (white), two torus (medium grey), three torus (light grey) or chaotic attractor (black). In the dark grey region all Lyapunov exponents are very small.

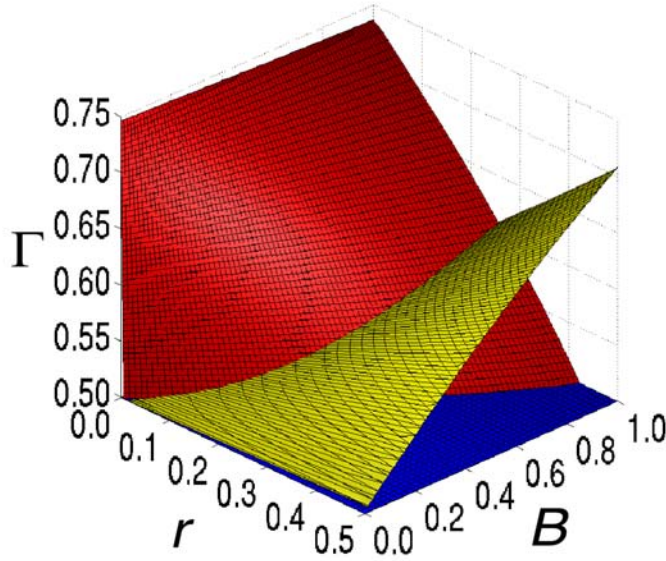


Figure 6.3: Bifurcation diagram of a four-trophic food chain with additional mortality terms for quadratic closure and moderate nutrient limitation. The parameters Γ and r denote the predators sensitivity to prey density and the relative length of timescales respectively. The parameter B is the portion of the biomass loss of species two and three that occurs because of predation. The diagram shows two Hopf bifurcation surfaces (red, green) and a general saddle-node bifurcation surface (blue). The normalized steady state is stable above the Hopf bifurcations and unstable below. Increasing the mortality terms (decreasing B) has a stabilizing effect on the stability of the food chain, but can not prevent the chaotic dynamics.

occurs because of predation. By contrast, $B \approx 0$ would mean that almost the entire biomass loss occurs because of the mortality terms.

In the bifurcation diagram in Fig. 6.3 the value of B has been varied. The surfaces in the diagram correspond to the two Hopf bifurcation surfaces and the general saddle-node bifurcation surface that have been shown in Fig. 6.1. Increasing the strength of the mortality (that is decreasing B) decreases the critical value of Γ at which the Hopf bifurcations occur. This stabilizing effect of mortality can be understood if one considers that high mortality weakens the interactions in the food chain.

As the strength of the mortality is increased the double Hopf bifurcation is shifted towards lower values of r . The double Hopf bifurcation line ends at $B = 0$. At this value of B both Hopf bifurcation surfaces vanish in Takens-Bogdanov bifurcation lines. The fact, that the double Hopf bifurcation line survives up to $B = 0$ this proves that chaos exists generically even in food chains with very strong mortality.

6.3.6 A degenerate double Hopf bifurcation

While the existence of chaos close to generic Hopf bifurcations has been proved many details on the transition to chaos remain uncertain (Kuznetsov 1995). Even less is known about degenerate double Hopf bifurcations. Since a degenerate double Hopf bifurcation is a codimension-three point very few examples from applications are known. In this section and the following we use our three parameter bifurcation diagrams to locate two examples of degenerate double Hopf bifurcations in general food chains.

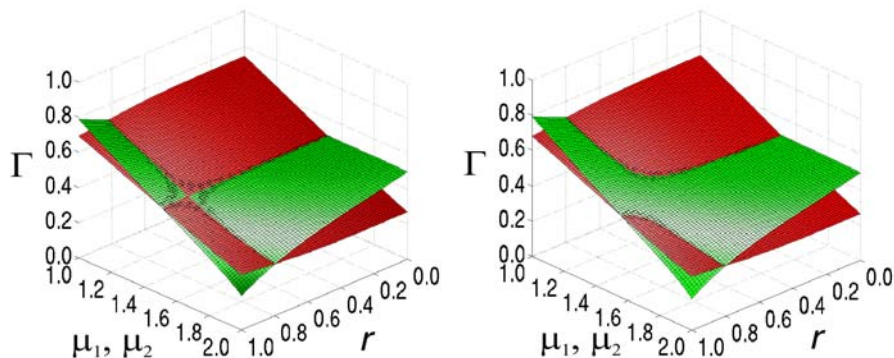


Figure 6.4: Bifurcation diagrams for a four-trophic food chain with $p = 1$ (left) and $p = 1.01$ (right). The steady state under consideration is stable above the Hopf bifurcation surfaces (red, green). For high values of the mortality exponents μ_2 and μ_3 the Hopf bifurcations occur at lower values of the predator's sensitivity to prey density Γ . This shows that high mortality exponents have a stabilizing effect on the food chain. At the intersection of the two Hopf bifurcation surfaces a double Hopf bifurcation is formed. For $p = 1$ the two double Hopf bifurcations cross in a degenerate double Hopf bifurcation point. However, this crossing is avoided for $p \neq 1$.

We investigate the local dynamics of four-trophic food chains with linear top-predator mortality ($p = 1$) and relatively strong mortality terms for the other predators ($b_2 = b_3 = 1/2$). The mortality exponents μ_2, μ_3 that correspond to these mortality terms are assumed to be identical. A bifurcation diagram for this food chain is shown as the left diagram in Fig. 6.4. The surfaces that appear in the diagram are the two Hopf bifurcation surfaces from Fig. 6.1. The general saddle node bifurcation surface would be located at $\Gamma = 0$ and is not shown. The diagram reveals that the Hopf bifurcation surfaces intersect in two double Hopf bifurcation lines. An intersection of the bifurcation lines occurs in the center of the diagram. At the intersection the double Hopf bifurcations become degenerate. Note that even in the degenerate double Hopf bifurcation only two pairs of non-hyperbolic eigenvalues exist. Additional non-hyperbolic eigenvalues can only appear if more than two bifurcation surfaces intersect. The degenerate

double Hopf bifurcation considered here is characterized by a lack of uniqueness of the bifurcation lines. We can guess that this degeneracy is caused by the violation of a transversality condition. A closer investigation would require the explicit computation of normal form coefficients in a specific example.

The crossing of the bifurcation lines can be avoided by making the closure term slightly nonlinear. The right diagram in Fig. 6.4 is almost identical to the one shown in Fig. 6.4. However, we have increased the exponent of closure from $p = 1$ to $p = 1.01$. As a result the degenerate double Hopf bifurcation point has vanished.

Degeneracies that only appear in isolated points do not effect our conclusions. While the implications of the degenerate double Hopf bifurcations are unclear we can still deduce the existence of a chaotic region from the neighboring generic double Hopf bifurcations. At present we can not draw any ecological conclusions from the presence of the degenerate double Hopf bifurcation. However, the degenerate bifurcation point computed here can serve as an example for future mathematical investigations. In these investigations further insights can be gained that may enable us to formulate further conclusions on the dynamics of general ecological models.

6.3.7 Whitney umbrellas in food chains

Other examples of degenerate double Hopf bifurcations are found in the points in which a line of double Hopf bifurcations ends. In Sec. 6.3.5 we have already noted that this occurs if one of the Hopf bifurcation surfaces vanishes in a Takens-Bogdanov bifurcation. Let us now discuss a bifurcation in which the double Hopf bifurcation line ends despite the fact that both Hopf bifurcation surfaces survive. The bifurcation diagrams shown in Fig. 6.5 corresponds to a four-trophic food chain with linear closure ($p = 1$). We consider moderate nutrient limitation ($\phi = 0.5$) and neglect the mortality terms for species two and three ($b_2 = b_3 = 1$). In contrast to the cases considered so far we vary the sensitivity of the second predator γ_2 independently of $\gamma_1 = \gamma_3$. Small variations in γ_2 do not alter the bifurcation diagrams qualitatively. However, in the parameter range in which γ_2 is very low and γ_1 and γ_3 is very high a second line of double Hopf bifurcations is formed. As soon as the value of γ_2 is increased beyond a critical value the double Hopf bifurcation line ends in a 1:1-resonant double Hopf bifurcation. In this codimension-3 point the two purely imaginary eigenvalue pairs of the double Hopf bifurcation are exactly identical. The topological shape of the Hopf bifurcation surfaces close to the 1:1-resonant double Hopf point is known as a Whitney umbrella.

The 1:1-resonant double Hopf bifurcation illustrates that the double Hopf bifurcation line may disappear as parameters are varied. However, in the investigation of food chains we find these bifurcations only in the parameter range where r and certain sensitivity parameters are large while other sensitivity parameters are very small. The 1:1-resonant double Hopf points mark the end of double Hopf bifurcation lines which only exist in this parameter range. By contrast, the double Hopf bifurcation line on which our ecological conclusions

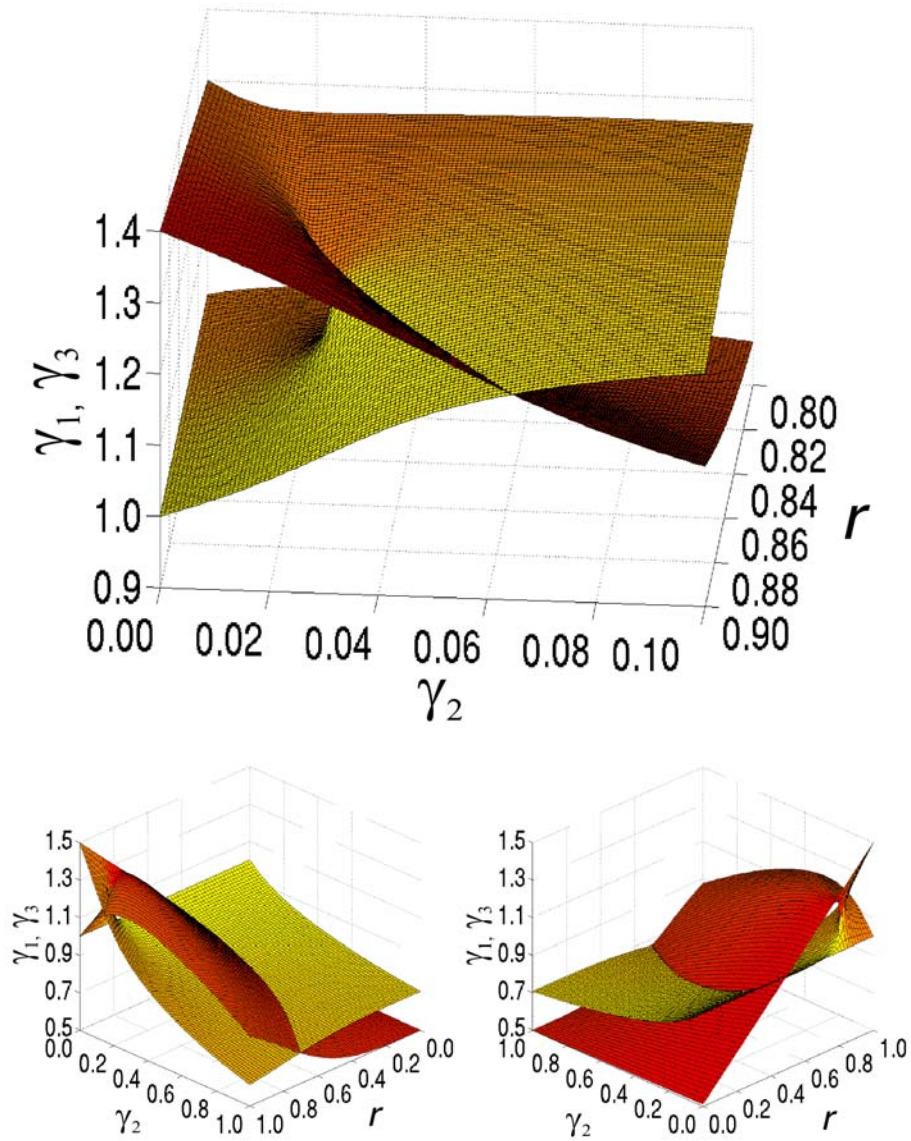


Figure 6.5: Bifurcation diagram of a four-trophic food chain. The diagrams show Hopf bifurcation surfaces which intersect in two double Hopf bifurcation lines. One of these lines ends in a 1:1-resonant double Hopf bifurcation. The parameters γ_1 , γ_2 and γ_3 describe the sensitivity of the predators to prey density while r denotes the relative length of the characteristic timescale of a predator compared to its prey. In the two lower diagrams the bifurcation surfaces are shown from different perspectives. The upper diagram shows the area around the 1:1-resonant double Hopf bifurcation in more detail.

are based is not effected. Small timescale separation as well as very low and very high sensitivity is rarely encountered in nature. The 1:1-resonant double Hopf bifurcation shown in Fig. 6.5 will probably not effect the dynamics of food chains found in nature. Nevertheless, it can serve as an example for mathematical investigations. Although it is in principle known that bifurcation surfaces can form Whitney umbrellas, examples for this type of behavior are very rare (Govaerts et al. 1997).

6.4 Mortality and Chaos in Food Chains

In this chapter we have shown that chaotic parameter regions generally exist in food chains of length four or more. This result holds independently of the specific functional form of the interactions and is therefore valid for a large class of different food chains. In particular, chaotic regions survive even in food chains with strong, nonlinear mortality terms.

Our results indicate that long food chains found in nature should be chaotic if chaotic dynamics are advantageous from an evolutionary point of view. In nature only few long food chains which consist of individual species have been observed. However, our results also apply to food chains in which the model variables represent groups of species, like in the models of Steele and Henderson (1992).

Despite the generic existence of chaos our analysis confirms that high exponents of closure and strong mortality have in general a stabilizing effect on steady states. In fact, there seems to be little relationship between the stability of steady states and the complexity of the dynamics that is observed after steady state stability has been lost. In this light it is misleading to call an effect stabilizing only because it causes a transition to less complex dynamics.

Chapter 7

Extension to Food Webs

In the previous chapters we have shown that general models can be used to study ecological questions with a high degree of generality. However, so far we have only been able to consider the dynamics of food chains in the general framework. In this chapter we extend the general approach to food webs.

Extensive investigations in the dynamics of food webs are beyond the scope of this work. Nevertheless, we discuss the extension of the general approach to food webs to illustrate the potential for future investigations. The emphasis of this chapter is therefore mainly on the actual derivation of the general food web model. The model is applied to study the competitive exclusion principle. In particular, we show that competitive exclusion can in general be avoided if nonlinear mortality terms or predator interference is taken into account. Our investigations on the dynamics of different food webs reveal that the local bifurcation diagrams of a large number of food webs are qualitatively similar to the bifurcation diagrams of food chains. The results that have been obtained in the previous chapters will therefore hold in a large class of food webs.

We start in Sec. 7.1 with a brief introduction that motivates our treatment of food chains. The derivation of the general food web model is presented in Sec. 7.2. Based on the results from this model we study the competitive exclusion principle in Sec. 7.3. The impact of different food web geometries is studied in Sec. 7.4. Some future extensions of the general food web model are outlined in Sec. 7.5. Finally we summarize this chapter briefly in Sec. 7.6.

7.1 Diversity and stability in food webs

While food chains have been extensively studied in models (Steele and Henderson 1992, Boer et al. 1998) and laboratory experiments (Kirk 1998, Fussmann et al. 2000) true food chains are rarely observed in nature. Instead, species interact in complex trophic networks, which are called *food webs*.

However, theoretical as well as experimental evidence indicates that the behavior of food webs should differ from the one observed in food chains. Theoretical investigations by May (1973) show that more complex ecological models exhibit in general more complex dynamics. Very diverse ecological systems in which a large number of species coexist should therefore exhibit very complex dynamics. However, in nature the opposite seems to be the case (Odum 1953, Elton 1958, MacArthur 1955). Diverse systems like the rainforest ecosystem seem to reside in a very stable steady state. But, simple systems like agricultural monocultures are prone to outbreaks of pests which frequently exhibit chaotic dynamics.

The striking difference between the diversity-stability relationship observed in models and the diversity-stability relationship observed in nature is known as the diversity-stability debate (McCann 2000). It has been pointed out that the solution to this debate lies in part in the fact that different types of stability are considered. The stability observed in nature is not the asymptotic stability that we have considered so far but stability in the sense of persistence (cf. Chap. 2). Nevertheless, the question how natural systems can be very diverse and very persistent at the same time remains open.

Several investigations indicate that the key to persistence lies in the food web geometry. For instance it has been shown by Yodzis (1981) that realistic food webs tend to be more stable than randomly generated ones. Furthermore, it has been shown by McCann et al. (1998) that a high number of weak interactions has a stabilizing effect on the food web.

An explanation for the apparent stability of food webs is provided by the so-called insurance hypothesis. According to this hypothesis the stability of natural food webs is caused by their redundancy (Yachi and Loreau 1999). This redundancy appears since many species occupy essentially the same ecological niche. It is argued that within an ecological niche the fluctuations of one species can be compensated by others. In this way the build-up of large fluctuations can possibly be avoided. In other words it is claimed that the coexistence of species in the same ecological niche stabilizes the ecological systems. However, on the other hand the competitive-exclusion principle says that stable coexistence of different species in the same steady state is impossible Gause (1934).

Despite the competitive exclusion principle the coexistence of similar species in non-stationary states is observed in many ecosystems. In fact, it has been shown by (Ebenhöh 1988, Armstrong and McGehee 1980 and others) that the coexistence of an arbitrary number of similar species in a non-stationary state is possible.

In summary we can say that the dynamics of natural food webs seem to reside in very persistent non-stationary states. In order to get a better understanding of how such a state is formed investigations with general models are desirable. However, the extension of our general model to food webs faces two difficulties. The competitive exclusion principle which seems to prohibit the existence of positive steady states in certain food webs. Even if steady states exist they may not be of ecological importance since the natural system is in a non-stationary state. In the following we address both of these difficulties. In Sec. 7.3 we

show that positive steady states generally exist despite the competitive-exclusion principle. Thereafter we show in Sec. 7.4 that a large class of food web models behave like food chains. In these models the steady state may be of ecological importance. Furthermore this result allows us to extend our conclusions on the generic existence of chaos to a large class of ecological models. In this way the analysis of steady states allows us to draw conclusions on the non-stationary dynamics.

7.2 A model for general food webs

In the derivation of the general food web model we follow essentially the same approach that we have applied for food chains. We formulate a system of ordinary differential equations which describes the dynamics of a general food web. In the second step the abundance and biomass flows in the steady state under consideration are normalized to one. Finally, we compute the Jacobian in the steady state and illustrate the general food web model with a simple example.

7.2.1 Formulation of the Model

Let us consider a general food web of N species. In analogy to the food chain model we denote the abundances of the species by X_1, \dots, X_N . The time evolution of the abundances is determined by a system of N ordinary differential equations. We can write these equations symbolically as

$$\dot{X}_n = \text{prod}_n - \text{mort}_n + \text{gain}_n - \text{loss}_n, \quad (7.1)$$

In this chapter the indices n , m and i will always run from 1 to N . The four terms on the right hand side of this equation correspond to primary production, mortality, biomass gains by predation and biomass losses because of predation (in this order). In the following we study these terms in more detail.

Production and mortality

In Eq. (7.1) we have included primary production terms in the differential equations of all species. This has been done since we do not want to define the number of primary producers in the model a priori. Instead, the primary production is modeled by a general function. We write

$$\text{prod}_n = S_n(\mathbf{X}) \quad (7.2)$$

The function $S_n(\mathbf{X})$ will in general vanish if n is not a primary producer. Likewise we can define the general mortality term

$$\text{mort}_n = D_n(\mathbf{X}) \quad (7.3)$$

Note that the mortality and the primary production of species n do not only depend on X_n but on the vector

$$\mathbf{X} = (X_1, \dots, X_N). \quad (7.4)$$

In this work we do not consider systems in which the mortality or primary production of one species depends on the abundance of another species. However, we include this possibility in the model as a basis for future investigations. Primary production terms that depend on different species arise for instance if two primary producers compete for an implicitly modeled nutrient. Another example is encountered in systems in which the primary producer recycles biomass that is lost by the other species in the food web. In this case the primary production depends in general on all losses and therefore on the abundances of all species.

Biomass gain through predation

The modeling of predation in food webs is more complex than the modeling of predation in food chains. In particular the situation in which a predator species feeds on more than one prey species gives rise to additional difficulties. In general it is not reasonable to consider the predation on different prey species as independent processes. Even if the predator feeds indiscriminately and simultaneously on the competing prey species the presence of one prey species effects the predation on the others. Let us illustrate this point in a simple example.

We consider a predator that feeds on two species 1 and 2. We assume that the predator can hunt for both prey species simultaneously. After a certain time the predator captures an individual of one of the prey species, say species 1. Assume that our predator needs some time to handle the prey after capture. During this time he can not hunt for further prey. That means the time in which the predator can hunt for species 2 is reduced as well. In this way species 2 benefits from the predator saturation caused by the presence of species 1.

The example shows that competing prey species interact indirectly by changing the saturation of their predator. The predation on multiple prey species can therefore not be described by separate response functions. Instead, one response function has to be used that depends on the abundance of all prey species. Several specific response functions that have been proposed for this purpose are discussed by Gentleman et al. (2003).

In our general food web model we avoid to restrict the predator-prey interaction to a specific functional form. However, we assume that the predator does not actively search for specific prey, but indiscriminately consumes all prey it can capture. This behavior is known as *passive switching*. In case of passive switching the amount of prey consumed by the predator species n depends only on the abundance X_n of the predators and the total amount of available prey. We denote the available prey by

$$H_n := \sum_{i=1}^N w_{i,n} X_i. \quad (7.5)$$

The constant parameters $w_{1,n}, \dots, w_{N,n}$ that appear in the equation describe the *preference* of the predator n to the respective prey species. The preference depends on a large number of biological details like for instance the success

probability for attacks of species n on species i . If the predator can not consume a given prey species at all the corresponding preference parameter vanishes.

Technically H_1, \dots, H_N are *auxiliary variables*. Such variables are introduced to write the model equations in a more concise way. Although we omit the argument \mathbf{X} , we have to keep in mind that the auxiliary variables represent *functions* of the state variables. Therefore partial derivatives of the auxiliary variable with respect to the state variables do not vanish.

In terms of X_n and H_n the total amount of prey consumed by the predator n can be written as a general function $F_n(H_n, X_n)$. These functions are analogous to the general response functions in the food chain model. Note however, that the numbering of the functions has changed.

The function $F_n(H_n, X_n)$ denotes the biomass that is consumed by species n . However, only a fraction η_n of the consumed biomass is converted into predator biomass. This yields

$$\text{gain}_n = \eta_n F_n(H_n, X_n) \quad (7.6)$$

Biomass loss because of predation

Let us now study the biomass loss of species n that arises because of predation. We start by considering the predation by a predator species i . Based on the results of the previous section we can write the total biomass consumed by that species as $F_i(H_i, X_i)$. We introduce a new auxiliary variable $Q_{n,i}$. This variable denotes the portion of the prey of species i that consists of individuals of species n . By applying Eq. (7.5) we can write

$$Q_{n,i} := \frac{w_{n,i} X_n}{H_i} \quad (7.7)$$

Note that H_i vanishes if species i is a primary producer. The definition Eq. (7.7) and several others below should therefore be interpreted in the sense of Eq. (4.6).

Since species n contributes a portion $Q_{n,i}$ to the available prey of species i it is reasonable to assume that it contributes the same portion to the amount of captured prey. We can therefore write the loss of species n that occurs because of predation by species i as $Q_{n,i} F_i(H_i, X_i)$. In order to determine the total biomass loss of species n we sum over all potential predators. This yields the term

$$\text{loss}_n = \sum_{i=1}^N Q_{n,i} F_i(H_i, X_i). \quad (7.8)$$

The normalized model

Let us summarize the results of this section. By applying Eq. (7.2), Eq. (7.3), Eq. (7.6) and Eq. (7.8) we can write Eq. (7.1) as

$$\dot{X}_n = S_n(\mathbf{X}) - D_n(\mathbf{X}) + \eta_n F_n(H_n, X_n) - \sum_{i=1}^N Q_{n,i} F_i(H_i, X_i). \quad (7.9)$$

7.2.2 Normalization

In order to analyze the local bifurcations of the general food web model we have to normalize the model. Like case of the food web model we assume that a positive steady state

$$\mathbf{X}^* = (X_1^*, \dots, X_N^*) \quad (7.10)$$

exists. This enables us to define normalized state variables

$$x_n := \frac{X_n}{X_n^*}. \quad (7.11)$$

Furthermore, we denote the auxiliary variables in the steady state by

$$H_n^* := H_n(\mathbf{X}^*), \quad (7.12)$$

$$\xi_{n,i} := Q_{n,i}(\mathbf{X}^*). \quad (7.13)$$

We can now define the normalized auxiliary variables

$$h_n := \frac{H_n}{H_n^*}, \quad (7.14)$$

$$q_{m,n} := \frac{Q_{m,n}}{\xi_{m,n}}. \quad (7.15)$$

and the normalized functions

$$s_n(\mathbf{x}) := \frac{S_n(\mathbf{X})}{S_n(\mathbf{X}^*)}, \quad (7.16)$$

$$d_n(\mathbf{x}) := \frac{D_n(\mathbf{X})}{D_n(\mathbf{X}^*)}, \quad (7.17)$$

$$f_n(h_n, x_n) := \frac{F_n(H_n, X_n)}{F_n(H_n^*, X_n^*)}. \quad (7.18)$$

The last of these definitions is not trivial since we have defined f_n as a function of h_n while F_n was a function of H_n . Nevertheless, it is always possible to define f_n in this way.

In order to derive a normalized ODE system we apply the definitions given above to rewrite Eq. (7.9). This yields

$$\begin{aligned} \dot{x}_n X_n^* &= s(\mathbf{x})S(\mathbf{X}^*) + \eta_n f_n(h_n, x_n) F_n(H_n^*, X_n^*) \\ &\quad - d_n(\mathbf{x})D_n(\mathbf{X}^*) - \sum_{i=1}^N q_{n,i} \xi_{n,i} f_i(h_i, x_i) F_i(H_i^*, X_i^*). \end{aligned} \quad (7.19)$$

Let us now consider this equation in the steady state $x_1^* = \dots = x_n^* = 1$. By applying the corresponding definitions we can confirm that

$$h_n^* = q_{m,n}^* = 1, \quad (7.20)$$

$$s_n(\mathbf{x}^*) = d_n(\mathbf{x}^*) = f_n(h_n^*, x_n^*) = 1. \quad (7.21)$$

This allows us to write Eq. (7.19) as

$$\alpha_n := \frac{S(\mathbf{X}^*)}{X_n^*} + \frac{\eta_n F_n(H_n^*, X_n^*)}{X_n^*} = \frac{D_n(\mathbf{X}^*)}{X_n^*} + \sum_{i=1}^N \frac{\xi_{n,i} F_i(H_i^*, X_i^*)}{X_n^*}. \quad (7.22)$$

Since only constants appear in Eq. (7.22) the equals sign holds even if the system is not in the normalized steady state. The left hand side of the equals sign describes the different forms of biomass gain while the right hand side describes the forms of biomass loss. We can interpret the parameter α_n that has been defined in Eq. (7.22) as the biomass production rate per unit biomass. On the other hand it also denotes the loss rate per unit biomass of species n . Like in Chap. 4 it is therefore reasonable to consider α_n as a characteristic timescale of species n . In addition to the characteristic timescales we define general parameters that characterize the branching of the biomass flow in the food web. We write

$$a_n := \frac{1}{\alpha_n} \frac{\eta_n F_n(H_n^*, X_n^*)}{X_n^*}, \quad (7.23)$$

$$b_{n,i} := \frac{1}{\alpha_n} \frac{Q_{n,i} F_i(H_i^*, X_i^*)}{X_n^*}, \quad (7.24)$$

$$\tilde{a}_n := 1 - a = \frac{1}{\alpha_n} \frac{S(\mathbf{X}^*)}{X_n^*}, \quad (7.25)$$

$$\tilde{b}_n := 1 - \sum_{i=1}^N b_{n,i} = \frac{1}{\alpha_n} \frac{D_n(\mathbf{X}^*)}{X_n^*}. \quad (7.26)$$

The *predation ratio* a_n of species n denotes the portion of the total biomass production of species n that is gained by predation. If species n is primary producer this parameter vanishes. By contrast, for predators the predation ratio is in general 1. The parameters $b_{n,1}, \dots, b_{n,N}$ of species n are similar to the branching ratios that have been defined in Chap. 4. The parameter $b_{n,i}$ indicates the total portion of the biomass loss of species n that arises because of predation by species i . The remaining portion \tilde{b}_n of the biomass loss of species n is caused by mortality.

In terms of the normalized variables the ODE system can be written as

$$\dot{x}_n = \alpha_n \left(\tilde{a}_n s(\mathbf{x}) + a_n f_n(h_n, x_n) - \tilde{b}_n d_n(\mathbf{x}) - \sum_{i=1}^N b_{n,i} q_{n,i} f_i(h_i, x_i) \right). \quad (7.27)$$

7.2.3 Stability of steady states

The next step in our analysis is the computation of the system's Jacobian. We proceed in two steps. In the first step we define additional general parameters in analogy to the food chain model. In the second step we compute the derivatives that appear in the Jacobian and identify the general parameters in these terms.

Definition of additional general parameters

We start by considering the primary production. The limitation of the primary producers by the nutrient supply can be described by the general parameters

$$\phi_{n,m} := \left. \frac{\partial}{\partial x_m} s_n(\mathbf{x}) \right|_{\mathbf{x}=\mathbf{x}^*}. \quad (7.28)$$

The diagonal parameters $\phi_{1,1}, \dots, \phi_{N,N}$ can be interpreted in the same way as the parameter ϕ in the general food chain model. For instance the parameter $\phi_{n,n}$ denotes the nutrient availability to the primary producer n . Since the food web consists of N species which have to be treated as potential primary producers, N such parameters exist.

In addition there are non-diagonal parameters $\phi_{m,n}$ with $n \neq m$. These parameters vanish unless the primary production of species n depends on the abundance of species m . A very similar situation is encountered for the mortality terms. We define the general parameters

$$\mu_{n,m} := \left. \frac{\partial}{\partial x_m} d_n(\mathbf{x}) \right|_{\mathbf{x}=\mathbf{x}^*}, \quad (7.29)$$

Again, the diagonal parameters correspond to the mortality exponents that have been defined in the food chain model. Non-diagonal parameters appear if the mortality of a given species depends on the abundance of other species.

Let us now consider predation. In the food chain model the parameters $\gamma_1, \dots, \gamma_{N-1}$ denoted the sensitivity of predators to the abundance of their prey. In order to define similar parameters in the food web model we have to consider the sensitivity of a predator n to the amount of available prey, that is h_n . We define

$$\gamma_n := \left. \frac{\partial}{\partial h_n} f_n(h_n, x_n) \right|_{\mathbf{x}=\mathbf{x}^*}. \quad (7.30)$$

In this equation a derivative with respect to h_n appears. Such derivatives do not turn up directly in the systems Jacobian. However, since h_n is an auxiliary variable we can write

$$\left. \frac{\partial}{\partial x_m} f_n(h_n, x_n) \right|_{\mathbf{x}=\mathbf{x}^*} = \left(\left. \frac{\partial}{\partial h_n} f_n(h_n, x_n) \right) \left(\left. \frac{\partial}{\partial x_m} h_n \right) \right) \Big|_{\mathbf{x}=\mathbf{x}^*}. \quad (7.31)$$

where $m \neq n$. The parameter γ_n appears as the first factor on the right hand side of Eq. (7.31). By applying Eq. (7.14), Eq. (7.5) and Eq. (7.13) we can write the second factor as

$$\left. \frac{\partial}{\partial x_m} \frac{H_n}{H_n^*} \right|_{\mathbf{x}=\mathbf{x}^*} = \frac{w_{m,n} X_m^*}{H_n^*} = \xi_{m,n}. \quad (7.32)$$

The parameter $\xi_{m,n}$ can be interpreted as the portion of the total prey of species n that is contributed by species m . For instance, if species m is the only prey of species n the value of $\xi_{m,n}$ is one. Using $\xi_{m,n}$ and γ_n we can write Eq. (7.31) as

$$\left. \frac{\partial}{\partial x_m} f_n(h_n, x_n) \right|_{\mathbf{x}=\mathbf{x}^*} = \gamma_n \xi_{m,n} \quad \text{for } m \neq n. \quad (7.33)$$

The corresponding equation for $m = n$ is

$$\left. \frac{\partial}{\partial x_n} f_n(h_n, x_n) \right|_{\mathbf{x}=\mathbf{x}^*} = \left. \frac{\partial}{\partial x_n} f_n(h_n^*, x_n) \right|_{\mathbf{x}=\mathbf{x}^*} + \gamma_n \xi_{n,n}, \quad (7.34)$$

where we have used that $f_n(h_n^*, x_n^*) = 1$. Eq. (7.34) describes the sensitivity of the feeding rate of a species n on its own abundance. In the food chain model we have interpreted the corresponding term as a measure of the competition within the predator population (cf. Sec. 4.2.4). However, in Eq. (7.34) only the first term on the right hand side describes intraspecific competition. By contrast the second term arises because of intraspecific predation, that is cannibalism. In order to keep our interpretation of the parameters consistent with the food chain model we measure the intraspecific competition in terms of the parameters

$$\psi_n := \left. \frac{\partial}{\partial x_n} f_n(h_n, x_n) \right|_{\mathbf{x}=\mathbf{x}^*} - \gamma_n \xi_{n,n}, \quad (7.35)$$

Computation of the Jacobian

Let us now investigate how these parameters appear in the Jacobian of the food web model. We start by considering the term

$$\left. \frac{\partial}{\partial x_m} Q_{n,i} \right|_{\mathbf{x}=\mathbf{x}^*} = \left. \frac{\partial}{\partial x_m} \frac{w_{n,i} X_n^* x_n}{\sum_{j=1}^N w_{j,i} X_j^* x_j} \right|_{\mathbf{x}=\mathbf{x}^*} \quad (7.36)$$

Explicit calculation of the derivatives reveals

$$\left. \frac{\partial}{\partial x_m} Q_{n,i} \right|_{\mathbf{x}=\mathbf{x}^*} = \frac{w_{n,i} X_n^*}{\sum_{j=1}^N w_{j,i} X_j^*} - \frac{w_{n,i} X_n^*}{(\sum_{j=1}^N w_{j,i} X_j^*)^2} w_{m,i} X_m^* \quad (7.37)$$

for $m = n$ and

$$\left. \frac{\partial}{\partial x_m} Q_{n,i} \right|_{\mathbf{x}=\mathbf{x}^*} = - \frac{w_{n,i} X_n^*}{(\sum_{j=1}^N w_{j,i} X_j^*)^2} w_{m,i} X_m^* \quad (7.38)$$

for $m \neq n$. We apply Eq. (7.13) to write this equation in the form

$$\left. \frac{\partial}{\partial x_m} Q_{n,i} \right|_{\mathbf{x}=\mathbf{x}^*} = \begin{cases} \xi_{n,i} - \xi_{n,i} \xi_{m,i} & \text{for } n = m \\ -\xi_{n,i} \xi_{m,i} & \text{for } n \neq m \end{cases} \quad (7.39)$$

This result enables us to write

$$\left. \frac{\partial}{\partial x_m} q_{n,i} \right|_{\mathbf{x}=\mathbf{x}^*} = \frac{1}{\xi_{n,i}} \left. \frac{\partial}{\partial x_m} Q_{n,i} \right|_{\mathbf{x}=\mathbf{x}^*} = \begin{cases} 1 - \xi_{m,i} & \text{for } n = m \\ -\xi_{m,i} & \text{for } n \neq m \end{cases} \quad (7.40)$$

In a similar way we use Eq. (7.35), Eq. (7.13) and Eq. (7.30) to obtain

$$\left. \frac{\partial}{\partial x_m} f_i(h_i, x_i) \right|_{\mathbf{x}=\mathbf{x}^*} = \begin{cases} \psi_i + \gamma_i \xi_{m,i} & \text{for } i = m \\ \gamma_i \xi_{m,i} & \text{for } i \neq m \end{cases} \quad (7.41)$$

Having completed these preparations we can now consider the derivatives of the sum in Eq. (7.27). For $m \neq n$ we obtain

$$\begin{aligned}
& \frac{\partial}{\partial x_m} \left(\sum_{i=1}^N b_{n,i} q_{n,i} f_i(h_i, x_i) \right)_{\mathbf{x}=\mathbf{x}^*} \\
&= \frac{\partial}{\partial x_m} \left(b_{n,m} q_{n,m} f_m(h_m, x_m) + \sum_{i \neq m} b_{n,i} q_{n,i} f_i(h_i, x_i) \right)_{\mathbf{x}=\mathbf{x}^*} \\
&= b_{n,m} (\psi_m + \gamma_m \xi_{m,m} - \xi_{m,m}) + \sum_{i \neq m} b_{n,i} (\gamma_i \xi_{m,i} - \xi_{m,i}) \\
&= b_{n,m} \psi_m + \sum_{i=1}^N b_{n,i} (\gamma_i - 1) \xi_{m,i}. \tag{7.42}
\end{aligned}$$

Analogously we find for $m = n$

$$\frac{\partial}{\partial x_m} \left(\sum_{i=1}^N b_{n,i} q_{n,i} f_i \right)_{\mathbf{x}=\mathbf{x}^*} = b_{n,m} \psi_m + \sum_{i=1}^N b_{n,i} (1 + (\gamma_i - 1) \xi_{m,i}). \tag{7.43}$$

By applying Eq. (7.28), Eq. (7.29), Eq. (7.31), Eq. (7.42) and Eq. (7.43) we can write the diagonal elements of the Jacobian as

$$\begin{aligned}
J_{n,n} &= \alpha_n (\tilde{a}_n \phi_{n,n} + a_n (\psi_n + \gamma_n \xi_{n,n}) - \tilde{b}_n \mu_{n,n}) \\
&\quad - \alpha_n b_{n,n} \psi_n - \alpha_n \sum_{i=1}^N b_{n,i} (1 + (\gamma_i - 1) \xi_{n,i}) \tag{7.44}
\end{aligned}$$

and the non-diagonal elements as

$$\begin{aligned}
J_{n,m} &= \alpha_n (\tilde{a}_n \phi_{m,n} + a_n (\gamma_n \xi_{m,n}) - \tilde{b}_n \mu_{m,n}) \\
&\quad - \alpha_n b_{n,m} \psi_m - \alpha_n \sum_{i=1}^N b_{n,i} (\gamma_i - 1) \xi_{m,i} \tag{7.45}
\end{aligned}$$

where $m \neq n$. Although Eq. (7.44) and Eq. (7.45) look quite complex they simplify the computation of general Jacobians considerably. Using symbolic algebra software like Maple it is possible to obtain the Jacobian for a general food web with the desired web geometry within minutes.

7.3 The competitive exclusion principle

In the derivation of the general food chain model we have assumed that positive steady states generally exist. While this assumption is reasonable for food chains it seems to be problematic in certain food webs. One could argue that the competitive exclusion principle generally prohibits steady states in which two or more species occupy the same position in the food web. In this section we show that this is not the case.

7.3.1 Competitive exclusion in specific models

Let us start with an example in which positive steady states do not exist. Consider the simple food web which is described by the equations

$$\dot{X}_1 = S(X_1) - X_2G(X_1) - X_3G(X_1), \quad (7.46)$$

$$\dot{X}_2 = X_2G(X_1) - M_2X_2, \quad (7.47)$$

$$\dot{X}_3 = X_3G(X_1) - M_3X_3. \quad (7.48)$$

In this system the species 2 and 3 feed on species 1. The predator species feed in a similar way but have different mortality rates M_2 , M_3 . We have assumed that the predation is prey dependent. That is, the predator abundance enters linearly in the predation rates.

Let us now try to compute the species' abundances in the steady state. We start by considering Eq. (7.47). Since we seek positive solutions we can write

$$G(X_1^*) = M_2. \quad (7.49)$$

However, in the same way Eq. (7.48) yields

$$G(X_1^*) = M_3. \quad (7.50)$$

Therefore it is in general impossible to solve Eq. (7.49) and Eq. (7.50) simultaneously. Even if the response functions of the two predators are different we end up with two equations which determine one variable. Mathematically speaking, the system is overdetermined. In general such a system can not be solved and hence a positive steady state does in general not exist.

The example considered above would pose a serious problem for our model if it described the generic situation found in nature. However, the absence of a positive steady state in the example is caused by a degeneracy in the structure of the model. This degeneracy disappears if the model is perturbed slightly. Let us for instance assume that the mortality of the predators is slightly nonlinear. Instead of Eq. (7.47) and Eq. (7.48) we write

$$\dot{X}_2 = X_2G(X_1) - M_2X_2^p, \quad (7.51)$$

$$\dot{X}_3 = X_3G(X_1) - M_3X_3^p. \quad (7.52)$$

The equations that correspond to Eq. (7.49) and Eq. (7.50) now read

$$G(X_1^*) = M_2X_2^{*p-1}, \quad (7.53)$$

$$G(X_1^*) = M_3X_3^{*p-1}. \quad (7.54)$$

For $p \neq 1$ these equations are not overdetermined. Therefore solutions generally exist. We can write the ratio of the predator abundances in the steady state as

$$\frac{X_2^*}{X_3^*} = \left(\frac{M_3}{M_2} \right)^{\frac{1}{p-1}}. \quad (7.55)$$

Note that the ratio X_2^*/X_3^* is positive for $p > 1$ as well as for $p < 1$. Therefore, a steady state in which both predators have positive abundances exists if $p \neq 1$.

In the case $p = 1$ the degeneracy arises since both predation terms and both mortality terms are assumed to be exactly proportional to the abundance of the predators. This degeneracy vanishes if one of the four terms is at least slightly nonlinear. In the previous chapter we have shown that a number of different effects can cause nonlinearities in the mortality rates. Nonlinear predation rates appear in models if the intraspecific interference between predators or other forms of social interaction is taken into account. Although such interactions may be very subtle (say, by chance two predators attack the same prey) they will in general introduce a small nonlinearity in the predator dependence of predation rates.

This does not imply that coexistence is always possible. The positive steady state can still become unstable or vanish in bifurcations. However, the fact that a positive steady states generally exist proves that general models can be applied.

7.3.2 Competitive exclusion in general models

Let us consider the effect of competitive exclusion on general food webs. In analogy to the example studied above we compute the general Jacobian of a system in which two predator species feed on one prey species. This yields

$$\mathbf{J} = \begin{pmatrix} \phi_{1,1} - b_{1,2}\gamma_2 - b_{1,3}\gamma_3 & -b_{1,2}\psi_2 & -b_{1,3}\psi_3 \\ \alpha_2\gamma_2 & \alpha_2(\psi_2 - \mu_{2,2}) & 0 \\ \alpha_3\gamma_3 & 0 & \alpha_3(\psi_3 - \mu_{3,3}) \end{pmatrix}. \quad (7.56)$$

If we assume linear predator mortality ($\mu_{2,2} = 1$, $\mu_{3,3} = 1$) and absence of predator interference ($\psi_2 = 1$, $\psi_3 = 1$) the Jacobian becomes

$$\mathbf{J} = \begin{pmatrix} \phi_{1,1} - b_{1,2}\gamma_2 - b_{1,3}\gamma_3 & -b_{1,2} & -b_{1,3} \\ \alpha_2\gamma_2 & 0 & 0 \\ \alpha_3\gamma_3 & 0 & 0 \end{pmatrix}. \quad (7.57)$$

In the Jacobian the third column can be obtained by multiplying the second column by $b_{1,3}/b_{1,2}$. Matrices in which one column (or row) is a linear combination of other columns (or rows) are *singular*. Such matrices always have at least one vanishing eigenvalue. The system that is described by the Eq. (7.57) appears to be in a general saddle-node bifurcation regardless of the remaining parameters in the Jacobian. However, if the system's structure is perturbed slightly, say, by taking nonlinear mortalities into account, the system leaves the bifurcation. Therefore any small perturbation can cause the transition to qualitatively different long term dynamics. Systems for which this is the case are *structurally unstable*.

To consider structurally unstable models can be reasonable if symmetries exist that enforce this type instability. However, in case of food webs we have

shown that the degeneracy of the system is caused by assumptions made in the model and not by symmetries of the natural system.

In the degenerate situation no positive steady state exists, therefore a central assumption that has been made in the derivation of the general model is wrong. Nevertheless, the general food web model predicts the saddle-node bifurcation that characterizes the degenerate situation correctly. Although this point needs further consideration we can understand this prediction if we take into account that the model remains valid arbitrarily close to the bifurcation. Therefore, in the limit the bifurcation in which the model breaks down may be reached. However, a more careful mathematical investigation of this limit is certainly desirable.

By computing the general Jacobians for different food web geometries one can confirm that degeneracies arise if a number of species interact with exactly the same predator and prey species. In this case the degeneracy described above will generally appear if the number of these species is larger than the sum of their common predator and prey species. However, these degeneracies can be avoided if either nonlinear mortality terms or the interference of predators is taken into account.

To justify the use of linear terms it is often argued that these terms are actually a first order Taylor approximation of the nonlinear terms observed in nature (May 1973). However, the degeneracy related to the competitive exclusion principle shows that the first order approximation is often not sufficient to describe the dynamics of natural systems correctly.

We can say that the mortality terms as well as the predation terms should in general be at least slightly nonlinear in the predator abundance. As a result positive steady states are generally present. Since the system is no longer degenerate the positive steady state will generally survive subsequent perturbations of the model. For example the positive steady state is present in models in which minor differences between the response functions of the predators exist.

7.4 First results on food webs

Our discussion of the competitive exclusion principle has shown that positive steady states generally exist in food webs. The general food web model allows us to study the stability of these steady states with a high degree of generality. In this section we illustrate this analysis by computing bifurcation diagrams for different food webs. The investigations presented in this section are still of preliminary nature. In particular the investigation of the complex food webs described below are still in a very early stage. Nevertheless, we present some results to illustrate the perspectives for future investigations.

7.4.1 Simple food webs

Let us start by considering the simple food web in which two species of predators feed on the same prey species. The general Jacobian for this type of food web has already been obtained in Eq. (7.56). The corresponding bifurcation diagram

is shown as the top left diagram in Fig. 7.1. In the bifurcation diagram we have assumed allometric timescales ($\alpha_1 = 1, \alpha_2 = r, \alpha_3 = r$), moderate nutrient supply ($\phi = 0.5$) and similar sensitivity to prey abundance ($\Gamma := \gamma_2 = \gamma_3$). The biomass flow branches symmetrically ($b_{1,2} = b_{1,3} = 0.5$). The interference of predators is neglected ($\psi_2 = 1, \psi_3 = 1$). Consequently, we have to take nonlinear mortalities into account to avoid competitive exclusion. For the sake of simplicity we assume that the mortality exponent of both predators is identical this mortality exponent is denoted by p .

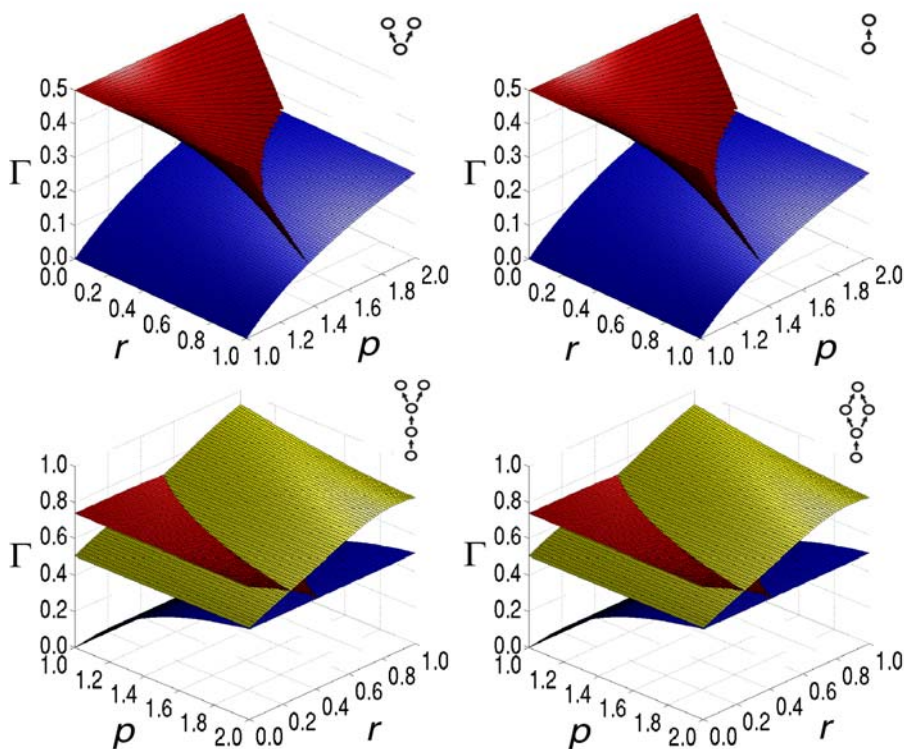


Figure 7.1: Bifurcation diagrams for simple food webs. The four bifurcation diagrams correspond to four food webs with different web geometries. The geometry under consideration is indicated symbolically in the top right corner of the diagrams. Although the geometries differ the two diagrams in the top row and the two diagrams in the bottom row are identical. In the diagrams Γ denotes the sensitivity of all predators to the density of their prey. The parameter p is the exponent of closure and r denotes the relative length of the prey timescales compared to the predator.

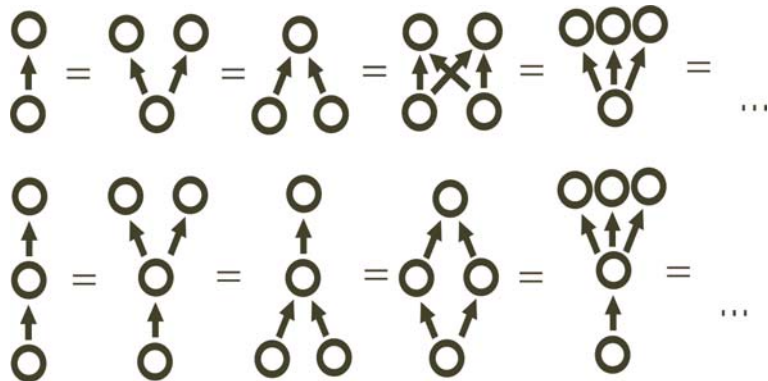


Figure 7.2: If similar parameters are considered the bifurcation diagrams of many food webs are identical to the bifurcation diagrams of a simple food chain with the same number of trophic levels. In this figure we indicate this identity by the ‘equals’ sign. The food webs are shown symbolically. Circles represent species while arrows indicate the biomass flow.

In the bifurcation diagram the positive steady state is stable in the top-most volume of the parameter space. If the sensitivity to prey Γ is decreased destabilization occurs either in a Hopf bifurcation (red surface) or in a general saddle-node bifurcation (blue surface). This saddle-node bifurcation surface is not the one that is related to the degeneracy described above. Since the degeneracy appears at $p = 1$ the corresponding bifurcation surface fills the $p = 1$ plane. In the figure this surface is not shown.

Let us compare the system to a simple di-trophic food chain. A bifurcation diagram for the food chain is shown as the top right diagram in Fig. 7.1. Both diagrams look very similar. In fact, we can use the method of resultants to prove that the Hopf bifurcation is in both diagrams located at

$$\Gamma = r(1 - p) + \frac{1}{2}. \quad (7.58)$$

Likewise, we find the general saddle-node bifurcation is in both diagrams at

$$\Gamma = \frac{p - 1}{2p}. \quad (7.59)$$

This proves that the two bifurcation diagrams in the top half of Fig. 7.1 are exactly identical. We can say that in terms of local asymptotic stability the system of with two competing predators behaves exactly like the food chain.

Under the assumptions made above the identity of bifurcation diagrams is observed in many examples. For instance the bifurcation diagrams in the lower half of Fig. 7.1 are identical to the bifurcation diagram of the simple four-trophic food chain shown in Chap. 6. Further examples for which this web-chain identity has been checked are shown symbolically in Fig. 7.2. We

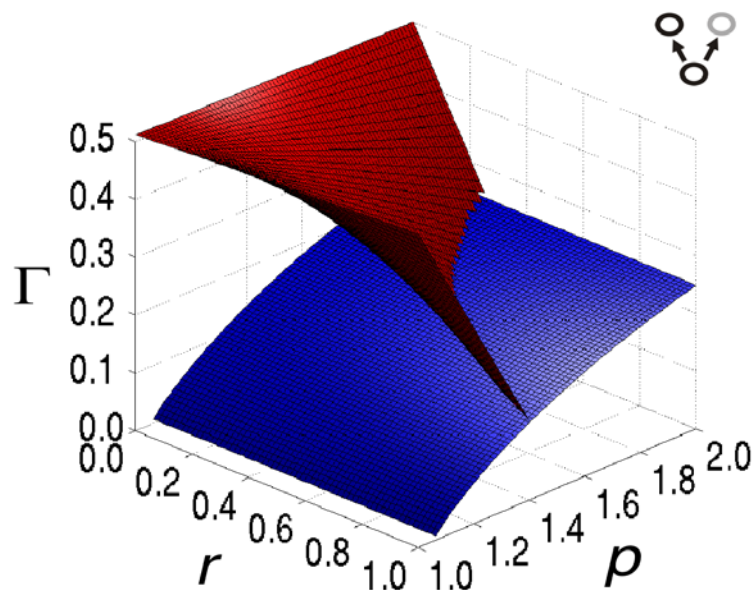


Figure 7.3: Local bifurcations of competing species with different general parameters. The diagram shows the Hopf bifurcation (red surface) and the general saddle node bifurcation (blue surface) that arise in a food web in which two predator species compete for one prey species. In contrast to the diagram shown in Fig. 7.1 the general parameters that describe the two competing species are chosen differently ($\alpha_1 = 1$, $\alpha_2 = r$, $\alpha_3 = 1.05r$, $b_{1,2} = 0.45$, $b_{1,3} = 0.55$, $\mu_{2,2} = p$, $\mu_{3,3} = 0.95p$, $\gamma_2 = 0.95\Gamma$, $\gamma_3 = \Gamma$). As a result the bifurcation surfaces move slightly. However the bifurcation diagram remains qualitatively identical.

can summarize the results of these investigations as a general rule: Identical bifurcation diagrams are encountered if a number of species which are described by identical general parameters occupy the same place in the food web. The local bifurcation diagram in which such species exist is identical to the diagram in which all species in one place are treated as one species.

In order to arrive at the general rule we have assumed that the general parameters that describe these species are exactly identical. While it is reasonable to assume that species that occupy the same place in a food web are described by similar values of the general parameters these parameters are in general not exactly identical. One could therefore suspect that the identity that appears in the examples is caused by yet another type of degeneracy. However, this is not the case. The general rule stated above can be extended to the case in which two species are not described by identical but by similar values of the parameters. Even if the parameter values are not exactly correct the local bifurcation diagrams of the full and the simplified system are qualitatively similar. In this light it appears reasonable to model food webs of similar species as food chains.

Let us illustrate this point by an example. Figure 7.3 shows another bifurcation diagram of the system in which two predator species feed on one prey species. However, this time all parameters that describe the competing predators have been chosen differently (s. figure legend). As a result the bifurcation surfaces in the diagram have moved slightly. However, the the number of the bifurcation surfaces and the shape of the individual surfaces remains unchanged. Although the bifurcation diagram is not exactly identical to the ones shown in Fig. 7.2 it is *qualitatively the same*. Qualitative differences arise only if very different species are considered.

The observed web-chain identity implies that our results on the dynamics of food chains will also hold for a large class of food webs. Whether the equivalence of food webs and food chains can be extended to global features of the dynamics remains to be seen. However, the fact that the higher codimension bifurcations are predicted correctly is promising.

7.4.2 Complex food webs

So far we have shown that *similar* species that occupy the same position in a food web can be treated as one species. However more complicated situations can arise if two *different* species occupy the same position in a food web.

Let us illustrate this point in a simple example. We consider a system in which two competing predator species feed on a single prey species. Both predator species are consumed by a top predator. In our model the prey species is species 1, the competing predators are species 2 and 3 and the top-predator is species 4. We assume that both predators are similar, but species 3 has some defense against the top predator that makes individuals of that species less likely to be consumed. If the defense is very weak the biomass loss of species 3 occurs mainly because of predation by the top-predator. In this case biomass loss because of mortality can be neglected. This situation corresponds to $b_{3,4} = 1$ and $\tilde{b}_3 = 0$. However, if the defense is very strong the biomass loss because of predation by the top predator can be neglected since almost all biomass loss occurs because of other mortality terms. In this case the general parameters are $b_{3,4} = 0$ and $\tilde{b}_3 = 1$. This illustrates that the parameter $b_{3,4}$ measures the strength of the trophic link between species 3 and the top predator. The top-predator is assumed to feed equally on species 2 and 3 if the defense of species 3 is weak. However, it feeds almost exclusively on species 2 if the defense of species 3 is strong. This is expressed by the relations

$$\xi_{3,4} = \frac{b_{3,4}}{2}, \quad (7.60)$$

$$\xi_{2,4} = 1 - \frac{b_{3,4}}{2}. \quad (7.61)$$

Furthermore we assume linear mortality terms ($\mu_{3,3} = 1, \mu_{4,4} = 1$). and moderate nutrient supply ($\phi_{1,1} = 0.5$). The timescales in the model are chosen in accordance to the usual allometric relation ($\alpha_1 = 1, \alpha_2 = r, \alpha_3 = r$,

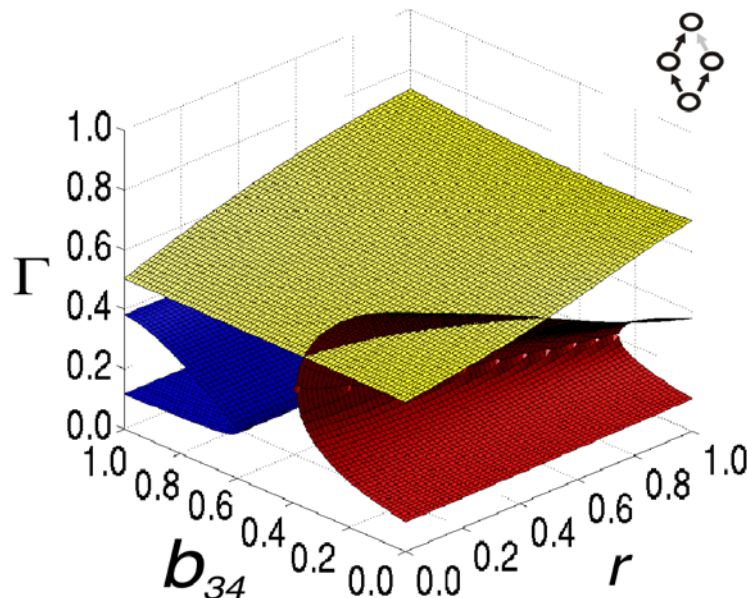


Figure 7.4: Bifurcation diagram of a food web with competing predators. In the diagram Hopf bifurcation surfaces (red, yellow) and a general saddle-node bifurcation surface (blue) appear. In addition to predator's sensitivity to prey density Γ and the relative length of timescales r the effect of the parameter $b_{3,4}$ is shown. This parameter measures the strength of the trophic link between one of the competing predators and the top-predator. For $b_{3,4} = 1$ the two competing predators are very similar. In this case the bifurcation diagram is qualitatively similar to a three-trophic foodchain. However, as $b_{3,4}$ is decreased the difference between the competing species grows and a additional Hopf bifurcation appears. As a result a double Hopf bifurcation is formed which indicates complex dynamics.

$\alpha_4 = r^2$). The sensitivity to prey density is assumed to be Γ for all predators ($\gamma_2 = \gamma_3 = \gamma_4 =: \Gamma$).

The effect of different values of $b_{3,4}$ on the local bifurcations is shown in Fig. 7.4. Let us start by considering the region in which the defense of species 3 is weak and $b_{3,4}$ is close to one. In this case the species are sufficiently similar to apply the general rule from the previous section. This rule predicts that the dynamics of the food web is qualitatively similar to the tri-trophic food chain. This is confirmed by the bifurcation diagram. For high values of $b_{3,4}$ one general saddle-node bifurcation surface (blue) and one Hopf bifurcation surface (red) appears in the diagram as one would expect in a tri-trophic food chain. However, as the parameter $b_{3,4}$ is decreased the difference between species 2 and 3 grows. At a certain point the species become too different to treat the system as a food chain. At low values of $b_{3,4}$ the general saddle-node bifurcation

surface disappears. Instead, we now find a second Hopf bifurcation surface (yellow). At the intersection of the Hopf bifurcation surfaces a double Hopf bifurcation is formed. In this region the bifurcation surfaces of the food web are roughly similar to the one that we have computed for the four-trophic food chain. However, the surfaces never become identical to the ones of the four-trophic chain.

Our results illustrate that it is reasonable to distinguish between simple and complex food webs. We call a food web simple if it can be modeled by an effective food chain with the same numbers of trophic levels. By contrast, this is not possible in complex food webs. While simple food webs behave qualitatively similar to the corresponding food chain complex food webs generally exhibit more complex behavior.

Bifurcation diagrams for two other examples of complex food webs are shown in Fig. 7.5. Both diagrams correspond to systems with three trophic levels. In tri-trophic food chains and simple three level food webs we would expect to find one Hopf bifurcation surface and one general saddle-node bifurcation surface. However, in complex food webs additional bifurcation surfaces appear. In both of the bifurcation diagrams two Hopf bifurcation surfaces and two general saddle-node bifurcation surfaces exist. As a result of the higher number of bifurcation surfaces double Hopf and Takens-Bogdanov bifurcations appear in both diagrams. Moreover, a Gavrilov-Guckenheimer bifurcation appears in the left diagram. The presence of these bifurcations shows that the dynamics of complex food webs is indeed more complex than the dynamics of simple food webs.

Both examples in Fig. 7.5 are tri-trophic systems which consist of five species. In the bifurcation diagrams the number and shape of the bifurcation surfaces in the diagrams is similar. But, certain differences exist. For instance a Gavrilov-Guckenheimer bifurcation appears only in the left bifurcation diagram. This demonstrates that the bifurcation structure of complex food webs is not determined by the number of species or trophic levels. Nevertheless, it may be possible to find general rules that predict the number of bifurcation surfaces in complex food webs. However, such an attempt exceeds the scope of the present work.

In general we can say that complex food webs contain at least as many bifurcation surfaces as the corresponding food chain with the same number of species. In many cases the number of bifurcation surfaces is higher. As a result many bifurcations of higher codimension are formed. These bifurcation lines indicate the presence of complex dynamics. Moreover, the topmost volume of parameter space becomes in many cases very small, so that the steady state is only stable in a small parameter region.

7.4.3 Stability despite complexity?

So far we have considered food webs which consist of a relatively small number of species. By contrast, the food webs observed in nature are far more complex. It can be argued that not every species in the natural food web needs to be modeled

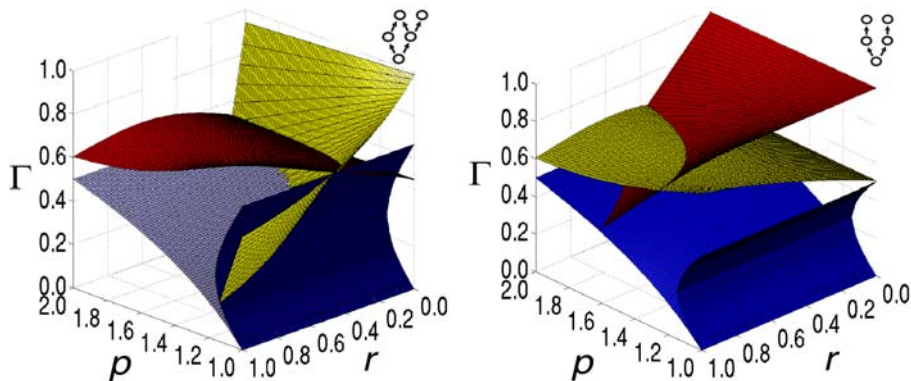


Figure 7.5: Local bifurcation diagrams for complex food webs. The two diagrams show the local bifurcations of two complex food webs. The surfaces correspond to Hopf bifurcations (red, green) and general saddle-node bifurcations (blue). In these diagrams more bifurcation surfaces appear than in simple food chains with the same number of levels. As a result the dynamics is generally more complex and the region in which the steady state is stable is smaller.

to describe the dynamics of natural systems. In fact, we can probably model many species together by applying the general rule which has been identified in Sec. 7.4.1. But, the fact that many weak trophic links exist in natural food webs (McCann et al. 1998) indicates that many species are too different to be grouped together.

Let us speculate on the way in which natural ecosystems could work. The theoretical results suggest that most complex ecological systems reside in a non-stationary state in which many species coexist. While the high degree of redundancy should make the system very persistent we can expect that the dynamics remains highly complex. However, an inherent feature of complexity is the appearance of emergent variables (Badii and Politi 1999). In contrast to the microscopic state variables the emergent variables often exhibit very simple dynamics. Consider for instance a volume of gas at rest. The individual gas atoms follow chaotic trajectories. However, the system as a whole can be described by emergent variables like pressure and temperature which behave in a much simpler fashion. This can explain the apparent stationarity of complex ecological systems. While the abundance of individual species may fluctuate in these systems emergent variables appear that exhibit simple dynamics.

In summary we can say that the stability of natural ecological systems arises probably from the interplay of a large number of *different* species. Since the complexity of these systems is an important inherent feature any model that attempts to describe such a system accurately has to be very complex as well. However, an accurate description may in many cases not be necessary. For many applications it is sufficient to consider models that describe the dynamics of emergent variables.

In fact, many ecological models have been formulated that describe the ecological dynamics not on the species level but on an emergent level. An example of such a model is the nutrient-phytoplankton-zooplankton food chain proposed by Steele and Henderson (1992). Other models describe the dynamics of functional groups in the plankton food web (Ebenhöh 1996). Such functional groups can be considered as emergent variables. In this sense the emergent dynamics of very complex ecological systems may be described by simple food chains or food webs.

In Chap. 4 we have shown that large uncertainties exist which make it difficult to describe the interaction of species with mathematical functions. In particular our investigation of the paradox of enrichment has revealed that models which rely on very simple mathematical functions may produce not reflect certain stability properties observed in the natural system. The attempt to derive a model that describes the dynamics of emergent variables is even more difficult. As a result most models apply the same simple mathematical functions that are used in models of interacting species. However, the mechanistic reasoning on which these functions are based may be inappropriate for emergent variables. In this light investigations with general models that do not rely on specific functional forms are desirable. The general food web model presented in this chapter provides a framework in which such investigations can be carried out.

7.5 Future investigations

In the investigations presented in this chapter we have focused on the impact of certain food web geometries on the dynamics. However, the general food web model can be used to study many other ecological questions with a high degree of generality. In this section we describe some ecological effects which can be studied in the present model or require only minor modifications.

Although we have studied different food web geometries there are certain important aspects of natural food webs which we have not considered so far. For instance cannibalism is already included in the model but has not been studied in this work. Another important feature that appears in many ecological systems is oligotrophy. In the examples presented here we have only considered predators which feed on prey species which are on the trophic level below their own. However, in nature oligotrophic predators which feed on prey species from different trophic levels are often observed. Like cannibalism oligotrophy is already possible in the general food web model but has not been considered here.

In order to consider other effects the interpretation of the variables has to be changed slightly. For instance we can include nutrients explicitly in the model by interpreting one model species as a nutrient concentration. As a result the corresponding parameter $\phi_{n,n}$ can no longer be interpreted as a measure of

nutrient availability. Instead, this parameter is now related to the inflow of nutrients into the system. Consequently, the dynamics at negative values of this parameter have to be studied.

A more profound reinterpretation of variables allows us to model the transition of individuals between different states. Think for instance of a species that occurs in two different spatial patches. In the general food web model we can describe the dynamics of such a species with *two* model species. While one model species is used to denote the population density in one location the other model species denotes the population density in the other location. The emigration of individuals from a given patch can be modeled as a mortality term $m_n(\mathbf{X})$ while the immigration should be modeled with the general production term $s_n(\mathbf{X})$. In a similar way other transitions can be modeled. For instance we can study the effect of a disease on a given species by using three model species to denote the number of susceptible, infected and recovered individuals. Other examples which can be treated similarly include the transition between different age classes or the transition between an active and an inactive state.

While explicit treatment of nutrients and the transition between different states only require a reinterpretation of certain variables other effects make minor extensions of the model necessary. For instance we have assumed that the efficiency of biomass conversion η_1, \dots, η_N and the timescales $\alpha_1, \dots, \alpha_N$ are constant. However, in principle such an assumption is not necessary in the derivation of the model. For instance we can assume that these parameters depend algebraically on the state variables. In this case the normalization can still be performed in a very similar way. However, in the course of this normalization additional general parameters will appear. A particularly interesting extension is to consider the prey preferences that depend algebraically the state variables. This extension would enable us to study predators that actively switch between different prey species.

Likewise, additional interactions can be taken into account. For instance we can consider predation terms that do not only depend on the abundance of predator and prey but also on other species. This would allow us to consider the effect of interspecific interference on the dynamics of the food web.

The most complex extensions of the model are those which involve the introduction of additional state variables. Such variables can be used to describe internal states of the species. This may be necessary to consider the effects of adaptation or evolution in the general model. Likewise the internal states may be used to denote the energy reserves of the species in addition to abundance. Additional state variables that are introduced for this purpose have to be normalized for the general analysis. However, the normalization procedure that we have applied for the species abundances can in spirit be extended to other variables as well.

7.6 Summary

In this chapter we have shown that positive steady states generally exist in food webs. The competitive exclusion principle does only prevent the existence of positive steady states in degenerate food webs in which the predator interference as well as the nonlinearity of the mortality terms is neglected.

The general food web model enables us to compute the stability of such states with a high degree of generality. The application of this model has revealed that a large class of food webs behaves qualitatively similar to food chains. The results that have been obtained in the previous chapters can therefore be extended to a large class of food webs. This result indicates that redundancy alone is not sufficient to stabilize the dynamics of simple food webs.

However, other food webs exist which exhibit more complex dynamics. These complex food webs consist of species that are too different to treat the system as a food chain. These food webs are in general characterized by complex dynamics.

The apparent stability of the food chains observed in nature can be explained with the appearance of emergent variables. These emergent variables can exhibit simple dynamics although the dynamics on the species level is complex.

Finally, we have shown that the general food web model can be applied to study a number of interesting ecological effects that have so far not been investigated with this level of generality.

Chapter 8

Conclusions

In this work we have formulated general models of ecological food webs and food chains. These models have enabled us to investigate ecological questions with a high degree of generality. We have studied the effect of enrichment on the local stability of steady states. Thereafter we have focussed on the question whether chaos generally exists in food webs. Finally, we have studied the effect of food web geometry on the local dynamics. Let us now discuss the results of this work and describe some perspectives for future investigations.

General models as a modeling approach

The idea behind the general models is to obtain a model with a high degree of generality by including only a very small amount of information. We have shown that models with this degree of generality can still be analyzed with the tools of local bifurcation theory. But, unlike specific models they can not be used to compute trajectories. As a result the predictions of general models can not be verified by the comparison to experimental data. However, there is in general little need to verify the model since the results depend only on very few assumptions. If verification is desired the bifurcations in the general model can be compared to the bifurcations in a specific model that the general model describes. This illustrates that general models do not predict the behavior of a particular system, but the behavior of a class of specific models.

Degeneracies in specific models

The investigation of the paradox of enrichment has revealed that models that are based on simple mathematical functions may not reflect certain dynamical properties observed in nature. Enrichment has always a destabilizing effect if the simple, commonly used response functions are employed in a given model. However, if more complex functions are used enrichment can have a stabilizing effect. We have shown that a large class of functions exists that exhibit this alternate type of behavior. In particular some of these functions are very similar to commonly used response functions. They can be derived from reasonable

biological assumptions. This means that biological species may escape the paradox of enrichment by adapting their behavior slightly. However, it also means that many simple models may not describe the stability of ecological systems correctly.

Our results on the paradox of enrichment are a strong motivation for the use of our general models. In these models we avoid to describe ecological processes by specific functions. This enables us to use general models to investigate the generality of conclusions from specific models. This analysis can reveal existence of the different types of model behavior as we have seen for the paradox of enrichment.

In some cases the general analysis shows that some type of behavior disappears if a specific model is perturbed slightly. For instance we have shown that such a degeneracy is related to the competitive exclusion principle. Despite this principle stable coexistence of competing species is generally possible if nonlinear mortality terms or interference of predators is taken into account. If both effects are neglected certain food web models become structurally unstable. In such a model any minor biological detail that is taken into account will cause the transition to qualitatively different long term behavior. It is therefore unlikely that degenerate, structural unstable models describe the generic dynamics observed in nature.

The fact that degeneracies can appear in specific models does not imply that such models should not be used. Specific models have provided many important insights and will continue to do so in the future. However, general hypotheses that are based on the investigation of specific models should be verified in a general context.

The abstract point of view

Our general models describe the local dynamics in terms of general parameters. The identification of these parameters is in itself an advantage. Our investigation of the paradox of enrichment has mainly focused on specific models. However, this analysis was based on the observation that the destabilizing effect of a enrichment is measured by the parameter Γ . In this way the identification of Γ in the general model has enabled us to compare the effects of enrichment in specific models.

In general we can say that the general parameters provide a natural coordinate system in which specific models can be compared. For instance the bifurcation diagrams shown in Chap. 7 have revealed that the local dynamics in certain food webs is qualitatively the same as the local dynamics in food chains. This web-chain identity would be much harder to spot if the bifurcations were not plotted in the general parameter space.

The observed web-chain identity has already enabled us to extend our results on food chain dynamics to a large class of food webs. Future investigations may reveal additional rules that determine the number of bifurcation surfaces in food webs. These general rules may in the long run evolve into a qualitative theory of food webs that helps to solve the complexity-stability question.

Linking ecology to bifurcation theory

The high degree of generality that characterizes the general models enables us to use results from bifurcation theory in a very general way. For instance we have used mathematical results on double Hopf bifurcations to prove that long food chains and many food webs generally exhibit chaotic dynamics in certain parameter regions. The chaotic regions survive even if strong nonlinear mortality terms are considered in the model.

Other bifurcations have similar implications. The Takens-Bogdanov bifurcation generally indicates the presence of a homoclinic bifurcations. Likewise, the Gavrilov-Guckenheimer bifurcation generally gives rise to quasiperiodic dynamics.

In the framework of the general model we can use results from bifurcation theory to draw ecological conclusions with a high degree of generality. At the same time the investigation of general ecological models provides new examples for mathematical investigations. For instance, our investigations in Chap. 6 have revealed that 1:1-resonant double Hopf bifurcations occur in the general food chain model. The ecological implication of this bifurcations are still unclear. However, they may be revealed in future mathematical investigations.

We can say that general models can bridge the gap between bifurcation theory and theoretical ecology. The investigations of general ecological models yields examples of higher-codimension bifurcations that appear in a whole class of ecological models. In return, the mathematical investigation of these bifurcations can reveal new ecological insights.

The method of resultants that we have used for the computation of Hopf bifurcations fits nicely in this mathematical background. The bifurcation diagrams that are shown in this work underline that the method of resultants is a powerful technique for the efficient computation of bifurcation surfaces. The application of this method in conjunction with computer algebra systems enables us to compute the bifurcation surfaces in an analytical way. Since no numerical calculations are needed the method can be applied in analytical proofs. In conjunction with general models the method can therefore be used to prove general ecological insights mathematically.

Future investigations

Since the general models depend on few assumptions their application is advantages in areas where large uncertainties exist and experimental measurements are difficult. In ecology these uncertainties arise from the complexity of the individual organisms and from the complexity of the system as a whole. We have already argued that the general food web model can be extended to investigate a large number of interesting ecological questions. However, other areas of science exist where similar or even greater uncertainties and difficulties exist. In these areas the application of general models is desirable. For instance general models could be used to study conceptual models from climate research, models of genetic networks or even models of social systems with a high degree of generality.

In this light general models can be regarded as a general modeling approach that can reveal interesting insights in many disciplines of science.

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Curriculum Vitae

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Education and Qualifications

since May 2001 PhD Student, Carl v. Ossietzky University, Oldenburg.
Thesis: *Population Dynamics: General results form local analysis.*

Sept. 1998 - May 2001 Diplom (MSc equivalent) in Physics, Carl von Ossietzky University, Oldenburg, Germany.
Thesis: *Impact Fusion as a Detector of Close-Range Scattering*,
Grade: *sehr gut (A)*

Sept 1997 - July 1998 Bachelor of Science in Physics, University of Portsmouth, Portsmouth, United Kingdom.
Thesis: *Computer-generated Holograms*
Grade: *1st class Honours*

Sept. 1995 - July 1997 Vordiplom, Carl von Ossietzky University, Oldenburg, Germany.
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May 1995 Abitur (A-level equivalent), Jade Gymnasium, Jaderberg.
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Publications

Articles

T. Gross, W. Ebenhöh and U. Feudel: Enrichment and Foodchain stability: the impact of different functional forms. *Journal of theoretical Biology* **227**, 349-358, 2004 .

T. Gross and U. Feudel: Analytical Search for Bifurcation Surfaces in Parameter Space. *Physica D* **195**, 292-302, 2004.

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M. Baurmann, T. Gross and U. Feudel: Instabilities and Pattern formation in simple ecosystem models. *In: BioGeoChemistry of Tidal Flats, FZ Terramare Berichte. 12*, 21-28, 2003.

Awards and Scholarships

Scholarships

Stipendiate of the *Studienstiftung des deutschen Volkes* (German National Scholarship Foundation). Student Grant 1997-2001, PhD Grant 2002-2004.

Awards

Bankleiterstipendium, Oldenburg, 2003.
Red Sock Award. SIAM Conference on application of dynamical systems 2003.
SIAM Student Travel Award. 2003.

Erklärung

Hiermit erkläre ich, dass ich diese Arbeit selbstständig verfasst und keine außer den angegebenen Hilfsmitteln verwendet habe.

Oldenburg den 07.08.2004

A handwritten signature in black ink, appearing to read 'Thilo Gross', written in a cursive style.

(Thilo Gross)