

Chapter 2

Mathematical Ecology

If we look at an ecosystem, we find a complex network of animals, plants, fungi, bacteria etc., exposed to all kinds of perturbation due to natural reasons as weather or due to man-made influences like pollution, agriculture, or harvesting. Nevertheless most ecosystems are astonishingly stable. Perhaps not every detail, but the overall structure is rather robust under perturbations. From a practical as well as from a theoretical point of view the mechanisms that lead to this stability are interesting to reveal. On the one hand ecosystems per se are investigated, and questions are asked like: why do predators stabilise an ecosystem, why do we find a lot of omnivores, why do similar species coexist though there is the principle of competitive exclusion? On the other hand, management and usage of ecosystems need a theoretical underpinning. Optimal harvesting does not loot the system but adapts the usage to sustain its structure. Conservation areas have to be planned carefully in size and spatial shape. In this chapter we will only sketch some of the most prominent results of this central field in mathematical biology; many more interesting results can be found in books exclusively devoted to this topic, and in research papers.

In order to approach our task, we start off with most simple models: only one single species inhabits an ecosystem. This seemingly extremely simple situation already leads to a lot of different modelling approaches and requires an astonishingly high mathematical effort. We then proceed to two-population models. Two populations may have different interaction patterns: one species may predate upon the other, the two species may compete for common resources, or they may help each other (mutualism). Even more complex is the situation if we have three species: we proceed towards the theory of food chains and food webs. Finally, we develop some methods to understand the complexity of even more complex food webs via the questions in how many different ways a system can have developed. Clearly, the larger the number of possible paths to a given food web, the more likely it is to observe it.

2.1 Single Species Models

The simplest case in mathematical ecology deals with one single homogeneous population, without any further structure. Starting from basic models we will refine the modelling approaches step by step, by including e.g. growth limitations, stochastic effects, time lags and further structures like temporal and spatial variability.

2.1.1 Exponential Growth

In this subsection, we briefly review the case of density-independent growth. Of course, in many applications, limited resources have a central influence. Nevertheless it is important to understand the basic principles of linear models used in ecology, on the one hand as they form the basis for a deeper understanding of the nonlinear setup, on the other hand as there are many situations that are well described by linear models (see also Chap. 1).

2.1.1.1 Linear Difference Equations

We only step very fast through linear and deterministic discrete-time models. There are examples of populations which are easily (and appropriately) to describe using discrete time. From a more ecological point of view, it is important to check, if the species in consideration is well-suited for a discrete-time description. One important criterion for the suitability of discrete-time models is: Do the births occur in regular time-intervals, e.g. caused by “breeding seasons”? Typical examples are (see [152]):

Monocarpic Plants (these are plants that grow, flower and produce seeds only once and then die). Many of these monocarps are annuals (like the sun-flowers), but there are also some which live for many years, e.g. Bamboos (with life times up to 100 years).

Semelparous Insects (insects that lay down eggs once in their life and die afterwards). Typical examples are mayflies and day-flies. There are also examples for long-living species, like some cicadas in eastern USA, with life times of 13 or 17 years.

Semelparous fishes. Some fishes also show semelparous behaviour and die soon after spawning (most well-known species are salmon and eels).

Iteroparous Birds (they can breed in more than one season). As birds often exhibit clearly-defined breeding seasons, they can often be described also by discrete-time models (maybe with an additional age structure).

Semelparous Mammals. There are not many, but at least some species showing semelparous behaviour. Examples are marsupials of the genus *Antechinus*, in this case, typically the males die after mating.

The basics of deterministic, discrete-time models were already introduced in Sect. 1.2.2, so we only recall a few topics in the context of ecology and start with the simplest case of a linear difference equation of first order, for one species.

Let x_n be the population size in the n -th generation. For the modelling approach we assume that each individual has (in average) $a \in \mathbb{R}_+$ descendants per generation, the so-called net reproductive number or net reproduction ratio (sometimes also wrongly called net reproduction rate; wrongly, because a is a number and does not carry the unit one over time as a rate does), then the linear model reads:

$$x_{n+1} = ax_n.$$

In case of iteroparous behaviour, one still can use $x_{n+1} = ax_n$ as model, but the factor a can be reinterpreted as $a = 1 + \beta - \mu$, where β is the average number of surviving births, and μ the probability of death per time interval.

The explicit solution reads

$$x_n = a^n x_0, \quad n \geq 1,$$

x_0 is the starting value. Following Definition 1.26, the stability and the qualitative behaviour of the solutions depends on the parameter a :

- For $|a| < 1$, $\bar{x} = 0$ is stable, for $|a| > 1$ it is unstable; $a = 1$ yields a constant sequence
- $a < 0$ leads to an alternating behaviour.

Of course, such a model is not realistic due to an unlimited growth in case of $a > 0$; nevertheless it can be useful e.g. to determine parameter values from data which are taken in a carefully chosen time span, where limitation of growth does not play a role.

2.1.1.2 Continuous Exponential Growth

Now we turn our attention to continuous time, but still consider deterministic behaviour. Let $x(t)$ describe the number of individuals which belong to the population. Then dx/dt denotes the “rate of change” and $\frac{1}{x}dx/dt = d\ln(x)/dt$ denotes the “per capita rate of change”. The per capita change is a key feature of a population model.

Central model assumption: The population size only changes due to births and deaths – e.g. immigration or emigration is not present. If we denote by β the per capita birth rate and by μ the per capita death rate, we obtain

$$\frac{1}{x} \frac{dx}{dt} = \beta - \mu.$$

By introducing the so-called “intrinsic rate of growth” $r = \beta - \mu$, this equation can be reformulated:

$$\frac{dx}{dt} = rx.$$

Including an initial condition

$$x(0) = x_0$$

(which describes the number of individuals which are present at the beginning of the observation) leads to an initial value problem, with a unique solution:

$$x(t) = x_0 e^{rt}.$$

Three cases can be distinguished:

- $r > 0$: exponential growth
- $r < 0$: exponential decay
- $r = 0$: constant population size

It is interesting to consider the dependency of e.g. the per capita growth rate and the (whole) population growth rate (Fig. 2.1). We observe: The per capita growth rate is constant – which means: there is no influence of the population size on the individuals and their “behaviour”. For the present model, the population growth rate is always increasing (which is not realistic for long times)!

There is just one stationary point: $x^* = 0$, which is obviously stable for $r < 0$, respectively unstable for $r > 0$.

In Fig. 2.2 experimental data from a bacterial growth experiment are shown, see the data in Table 2.1. The simple exponential growth model can be fitted quite well to the experimental data; at the last shown data point, one can recognise already the beginning of saturation, i.e., the exponential growth assumption starts to fail. The figure was created by simBTUM, the corresponding code can be found in the Appendix.

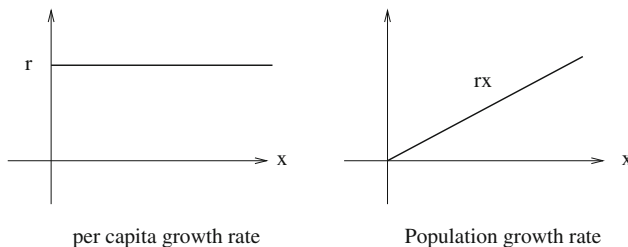


Fig. 2.1 Per capita growth rate and population growth rate for continuous exponential growth

Fig. 2.2 Comparison of experimental data (bacterial growth of *Pseudomonas putida* in units of cells/ml over time (hours), taken from [67]) with the exponential growth model

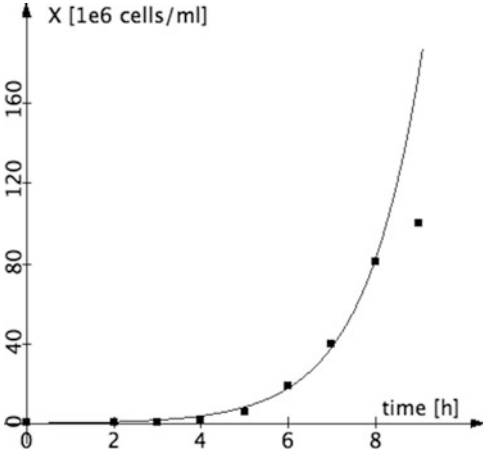


Table 2.1 Experimental data from a bacterial growth experiment with *Pseudomonas putida* (Taken from [67])

Time (h)	0	2	3	4	
Number of cells/ml	$3.36 \cdot 10^5$	$5.00 \cdot 10^5$	$8.00 \cdot 10^5$	$1.46 \cdot 10^6$	
Time (h)	5	6	7	8	9
Number of cells/ml	$6.00 \cdot 10^6$	$1.89 \cdot 10^7$	$4.00 \cdot 10^7$	$8.10 \cdot 10^7$	$1.00 \cdot 10^8$

2.1.1.3 Linear Birth and Death Process

As mentioned before, by using deterministic equations like $\frac{dx}{dt} = rx$ or later the deterministic logistic growth model $\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right)$, random influences are ignored, but they may be important for the growth of populations, especially, if the size of the population is quite small (then the influence of single individuals is large, see e.g. [152], or Sect. 1.1.4.3).

If a population is quite small, stochastic fluctuations may play a big role. As introduced already in Chap. 1, a simple population dynamics for one population can be well described by the birth-death process. Shortly, the master equations describe the probabilities to find the population at time t in state i . The corresponding generating function is useful for the solution. From an ecological point of view, the most essential things are:

- In contrast to the deterministic approach, the probability for extinction is also positive if the birth-rate is larger than the death-rate.
- Additional to the time course of the expected value for the population, it is possible to get information about the variance.

2.1.1.4 Conclusion

The expected value for the birth death process of independent individuals equals the corresponding deterministic exponential growth model. If a deterministic or stochastic approach should be taken depends on the population size and the question at hand: a small population size forces a stochastic approach, while large populations also allow to consider deterministic models. The deterministic models are more simple, but contain less information. Variances or probability for extinction can be only computed in the stochastic framework.

2.1.2 *Limited Resources*

In the last subsection, it was assumed that there are unlimited resources for population growth, that means that the increase is proportional to the present population (leading to the exponential growth), or the per capita birth rate is constant and density-independent. This assumption is justified only for certain populations, e.g. at the time a species successfully invades an ecosystem. In this section, we take into account that in most realistic situations, limitation of growth plays a big role. Furthermore, we should deal with the question about the origin of the limitation. Historically, two main hypotheses were considered (for more information see [152]):

- Hypothesis I: “biotic factors” are the main limiting factor; e.g. competition for resources. These factors have a bigger influence in case of large populations.
- Hypothesis II: “abiotic factors” like weather changes play a major role – they influence small populations in the same way as large populations.

Of course, both factors play a role in real life. Before setting up a model, one has to check carefully the most important factors in the concrete situation, and include these in the model. Here, we restrict ourselves to deal with Hypothesis I, i.e., the density-dependent regulation, as this is more concrete and interesting in our context. Typically, a limiting carrying capacity of the underlying ecosystem, due to lack of nutrients, living space etc. is assumed. Similar as above, one can choose a suitable modelling approach by deterministic or stochastic models.

2.1.2.1 Theoretical Background for Nonlinear Difference Equations of First Order

Here we introduce some basics for nonlinear discrete models. In general, $x_{n+1} = f(x_n)$ is denoted to be a difference equation of first order, and $f(\cdot)$ is called update function. As usual, stationary points and their stability are of interest. In this context

we use the following definitions:

Definition 2.1 \bar{x} is called stationary point of the system $x_{n+1} = f(x_n)$, if

$$\bar{x} = f(\bar{x}).$$

\bar{x} is also called fixed point or steady state.

For difference equations, the stability is defined via convergence of sequences:

Definition 2.2 Let \bar{x} be a stationary point of the system $x_{n+1} = f(x_n)$.

\bar{x} is called locally asymptotically stable, if there exists a neighbourhood U of \bar{x} such that for each starting value $x_0 \in U$ we obtain:

$$\lim_{n \rightarrow \infty} x_n = \bar{x}.$$

\bar{x} is called unstable, if \bar{x} is not (locally asymptotically) stable.

The following proposition yields a practical criterion for checking the stability:

Proposition 2.3 Let f be differentiable. A stationary point \bar{x} of $x_{n+1} = f(x_n)$ is

- Locally asymptotically stable, if $|f'(\bar{x})| < 1$
- Unstable, if $|f'(\bar{x})| > 1$

Proof (idea) We consider a stationary point \bar{x} of the difference equation $x_{n+1} = f(x_n)$. Then, one is interested in the local behaviour near \bar{x} . For this purpose, we consider the deviation of the elements of the sequence to the stationary point \bar{x} :

$$z_n := x_n - \bar{x}$$

z_n has the following property:

$$\begin{aligned} z_{n+1} &= x_{n+1} - \bar{x} \\ &= f(x_n) - \bar{x} \\ &= f(\bar{x} + z_n) - \bar{x}. \end{aligned}$$

Let the function f be differentiable in \bar{x} , thus we get $\lim_{h \rightarrow 0} \frac{f(\bar{x}+h) - f(\bar{x})}{h} = f'(\bar{x})$ and $f(\bar{x} + h) = f(\bar{x}) + h \cdot f'(\bar{x}) + O(h^2)$. This yields:

$$\begin{aligned} z_{n+1} &= f(\bar{x} + z_n) - \bar{x} \\ &= f(\bar{x} + z_n) - f(\bar{x}) \\ &= z_n \cdot f'(\bar{x}) + O(z_n^2). \end{aligned}$$

$O(z_n^2)$ is very small and can be neglected, i.e.,

$$z_{n+1} \approx z_n \cdot f'(\bar{x}),$$

which is again a linear difference equation, where we already know the criterion for stability and can apply it. \square

Remark This criterion is sufficient, but not necessary!

2.1.2.2 Graphic Iteration or “Cobwebbing”

Cobwebbing is a graphical method for drawing solutions of discrete-time systems (see e.g. [1]). It can give a first impression about the existence of stationary points and their stability. The proceeding is as follows, see also Fig. 2.3:

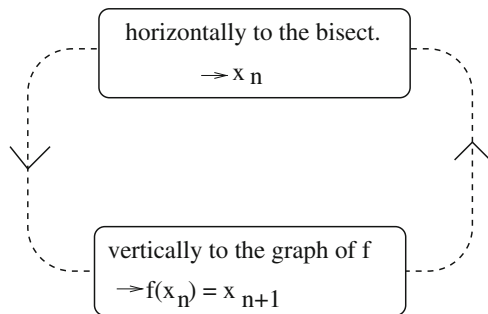
- Draw the graph of f and the first bisecting line in a coordinate system. Obviously, cutting points correspond to stationary points.
- Choose a starting value x_0 and the corresponding $f(x_0)$.
- For the iteration: draw a horizontal line to the bisecting line, from there a vertical line to the graph of f .

As an example, we consider a non-homogeneous linear model:

$$x_{n+1} = ax_n + b.$$

It can be interpreted as a population model with a constant reproduction rate a and a constant supply/removal b ; e.g. x_n as fish population at time step n , then $b < 0$ describes harvesting. Dependent on the parameter values for a , the qualitative behaviour in the neighbourhood of the stationary point $\bar{x} = b/(1 - a)$ changes, which can be seen very nicely by cobwebbing, Fig. 2.4.

Fig. 2.3 Iterative procedure for Cobwebbing



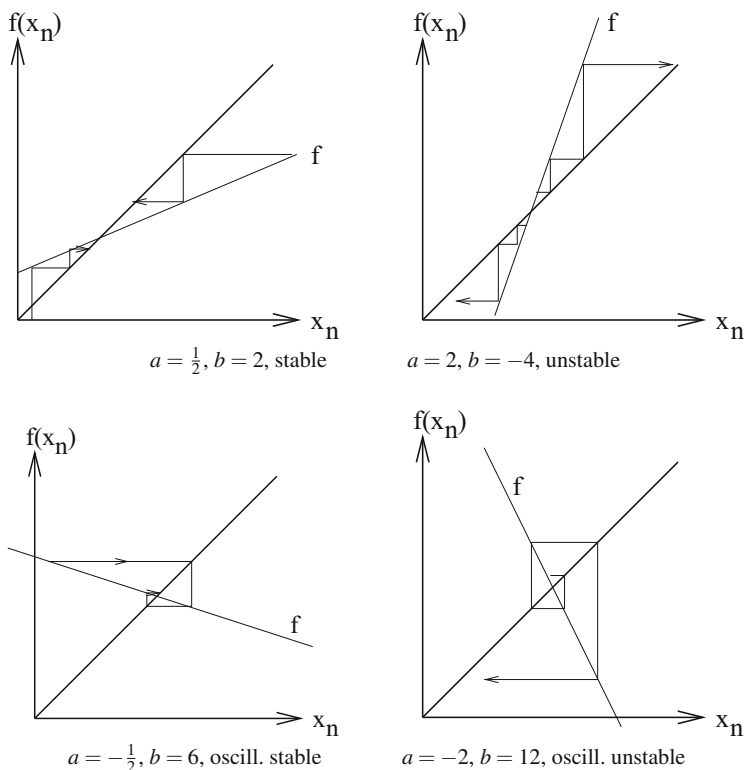


Fig. 2.4 Cobwebbing examples for a linear update function $f(\cdot)$

2.1.2.3 Sarkovskii Theorem

Concerning the discussion about the existence of orbits with different periods (for the logistic equation) we want to have a look for some more general results. Some of these theorems and observations are mentioned without proofs, they can be found e.g. in [123, 143]; a very nice and elementary introduction into phenomena related to iterating a map (not only this theorem but e.g. also about chaos or the kneading theory) is the book of Devaney [43]. The Theorem of Li and Yorke deals with a more general class of maps of intervals which includes the discrete logistic equation (2.1) introduced below as an important special case. The theorem shows that the discrete logistic equation can exhibit chaotic behaviour, which means that for a given parameter set periodic orbits with any period are present.

Formulating this more precisely, one can use this approach:

Remark 2.4 Mostly, chaos for a map f which iterates a metric (topological) space (X, d) is defined by the following three topological properties:

1. Transitivity: A function f is called transitive if for any non-empty open sets $U, V \subset X$, there is a $n \in \mathbb{N}$ such that $f^{(n)}(U) \cap V \neq \emptyset$. This implies that the map f mixes the complete set X quite well.
2. Sensitivity: There is a $\delta > 0$ such that for any $x \in X$ and neighbourhood $U(x)$ of x , there is $y \in U$ and $n \in \mathbb{N}$ such that $d(f^{(n)}(x), f^{(n)}(y)) > \delta$.
3. Periodic points are dense.

The Theorem of Li and Yorke focuses on the third property. The idea behind is that predicting the future of the system is rather difficult – the essential point for all definitions of chaos – as any period is present.

Theorem 2.5 (Theorem of Li and Yorke) *Let $f : \mathbb{R} \rightarrow \mathbb{R}$ be continuous. If f possesses a periodic point of period 3, then f possesses also periodic points of all other periods.*

Proof We start with two preliminary observations:

- Let $I, J \subset \mathbb{R}$ be closed intervals satisfying $I \subset J$ and $J \subset f(I)$, then f possesses a fixed point in I (this follows immediately from the intermediate value theorem).
- Let A_0, A_1, \dots, A_n be closed intervals satisfying $A_{i+1} \subset f(A_i)$ for $i = 0, \dots, n-1$, called “ $f(A_i)$ covers A_{i+1} ”, or, in symbols: $A_i \rightarrow A_{i+1}$. Starting with A_0 , there exists a subinterval J_0 of A_0 with $f(J_0) = A_1$. Similarly, there exists a subinterval of A_1 which is mapped onto A_2 . Hence, there exists a subinterval $J_1 \subset J_0$ with $f(J_1) \subset A_1$ and $f^2(J_1) = A_2$. This idea can be extended and we get a nested sequence of intervals $J_i \subset A_0$ which is mapped onto A_i , $i = 0, \dots, n$. As an immediate consequence of this observation we find from

$$A_0 \rightarrow A_1 \rightarrow \dots \rightarrow A_n \rightarrow A_0$$

that there is a fixed point $x \in A_0$ for $f^{(n)}(\cdot)$, where $f_i(x) \in A_i$ for all $i = 0, \dots, n$.

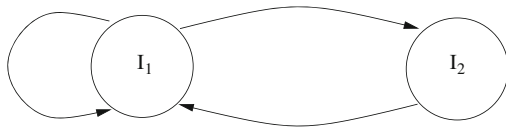
Now let $a, b, c \in \mathbb{R}$ with $a < b < c$ and $f(a) = b, f(b) = c, f(c) = a$, i.e., $\{a, b, c\}$ forms an orbit of period 3 of f . (The alternative case with $f(a) = c, f(c) = b, f(b) = a$ can be treated analogously.)

Let $I_0 = [a, b], I_1 = [b, c]$, this yields by assumption (see also Fig. 2.5):

$$\begin{aligned} I_1 \subset f(I_0) &\Rightarrow I_0 \rightarrow I_1 \\ I_0 \cup I_1 \subset f(I_1) &\Rightarrow I_1 \rightarrow I_1, \quad I_1 \rightarrow I_0 \cup I_1. \end{aligned}$$

From $I_1 \rightarrow I_1$ we conclude that there is a fixed point of $f(\cdot)$ (this is, a period one point). The graph $I_0 \rightarrow I_1 \rightarrow I_0 \cup I_1$ indicates a fixed point of $f^{(2)}(\cdot)$ in I_0 that is mapped by $f(\cdot)$ into I_1 . This is, this fixed point of $f^{(2)}(\cdot)$ is a proper period-two point. Similarly, we are able to construct period- n points with an arbitrary period

Fig. 2.5 Transition graph for the Theorem of Li and York



larger than two: consider the path

$$I_0 \rightarrow \underbrace{I_1 \rightarrow \cdots \rightarrow I_1}_{n-2 \text{ steps}} \rightarrow I_0 \cup I_1.$$

There is a fixed point $\hat{x} \in I_0$ of $f^{(n)}(\cdot)$ with $f^{(i)}(\hat{x}) \in I_1$ for $i = 1, \dots, n-1$. As $\hat{x} \in I_0$ only returns after n steps to I_0 , this point is a proper period- n point. \square

The assumptions of the Theorem of Li and Yorke do not claim the stability of the orbit of period 3, and there is nothing said about the stability of all the other periodic orbits. In concrete cases most of these orbits are unstable. Nevertheless, the Theorem of Li and Yorke yields an applicable criterion for a complex dynamic.

Even though the Theorem of Li and Yorke (1975) seems to be quite astonishing, it is only a special case of the Theorem of Sarkovskii (dating back to 1964). It is a very nice result, which depends only on the continuity of the considered function. For the formulation of this theorem we introduce a special order on the integers.

Definition 2.1 (Sarkovskii ordering) The so-called Sarkovskii ordering of the natural numbers is given by

$$3 \triangleleft 5 \triangleleft 7 \triangleleft \dots \triangleleft 2 \cdot 3 \triangleleft 2 \cdot 5 \triangleleft 2 \cdot 7 \triangleleft \dots \triangleleft 2^2 \cdot 3 \triangleleft 2^2 \cdot 5 \triangleleft \dots \triangleleft 2^n \cdot 3 \triangleleft \\ \triangleleft 2^n \cdot 5 \triangleleft \dots \triangleleft \dots \triangleleft 2^3 \triangleleft 2^2 \triangleleft 2^1 \triangleleft 1$$

In words: First comes the 3, then all other odds in ascending order, then all odds multiplied with 2, then all odds multiplied with the powers of 2 and so on. Finally, the pure powers of 2 are listed, in descending order. The Sarkovskii ordering can be applied very usefully to show the existence of orbits of certain periods.

Theorem 2.6 (Sarkovskii) Let $f : \mathbb{R} \rightarrow \mathbb{R}$ be a continuous function. If the system $x_{n+1} = f(x_n)$ possesses a periodic orbit of minimal period p , and $p \triangleleft q$, then it also shows up a periodic orbit of minimal period q .

We do not prove this Theorem; an elementary proof can be found e.g. in [43]. The special case $p = 3$ covers the Theorem of Li and Yorke. In a similar way a period 2^n indicates that there are points of order $2^{n'}$, $n' < n$. This latter result will be found back in the discussion of the period doubling route to chaos below.

2.1.2.4 Discrete Logistic Equation

The unlimited growth of a population is unrealistic, since a habitat has only a limited capacity. We will try to reflect this important point in a suitable model [58]. The “old” linear model can be reformulated in the following way:

$$\begin{aligned}x_{n+1} &= rx_n - \mu x_n \\ &= x_n(r - \mu),\end{aligned}$$

where $r = 1$ is the reproduction number. We now assume the probability for death μ to be proportional to the number of individuals, $\mu(x) = d x$ (the more individuals, the higher the death probability). The death term grows for large x faster than the birth term. In consequence, the per capita net growth is linearly decreasing in the population size, leading to

$$x_{n+1} = x_n(r - \mu x_n) = rx_n(1 - \frac{d}{r}x_n) = rx_n(1 - \frac{x_n}{K}),$$

where $\frac{\mu}{r} = \frac{1}{K}$. K is the carrying capacity of the habitat. The equation is simplified by measuring the population size in terms of the maximal population. Let $\tilde{x}_n = x_n/K$, then $\tilde{x}_n = r\tilde{x}_n(1 - \tilde{x}_n)$ which in some sense corresponds to the choice $K = 1$; this finding is natural, as we use K as the appropriate unit to measure the population size. We drop the tilde again, and work with

$$x_{n+1} = rx_n(1 - x_n). \quad (2.1)$$

Even if r is non-negative, $\mathbb{R}_+ = \{x \geq 0\}$ is not positively invariant in general. E.g. for $x_i > 1$, x_{i+1} becomes negative. Furthermore, it is easy to see that for $r > 4$ and $x_i = \frac{1}{2}$, $x_{i+1} = \frac{r}{4}$ there show up negative values. It is sensible to restrict ourselves to

$$0 \leq r \leq 4$$

such that the right hand side function $f(x) = rx(1 - x)$ maps the interval $[0, 1]$ into itself.

Due to nonlinearity, there may exist several fixed points:

$$\begin{aligned}\bar{x} &= f(\bar{x}) \Leftrightarrow \bar{x} = r\bar{x}(1 - \bar{x}) \\ &\Leftrightarrow \bar{x}[1 - r(1 - \bar{x})] = 0 \\ &\Leftrightarrow \bar{x}_1 = 0 \text{ or } 1 - r(1 - \bar{x}) = 0 \Leftrightarrow \bar{x}_2 = 1 - \frac{1}{r}.\end{aligned}$$

\bar{x}_2 is positive and therefore biologically relevant only for $r > 1$.

For the analysis of the stability we consider the first derivative, $f'(\bar{x}) = r - 2r\bar{x}$. For $\bar{x}_1 = 0$ we have $f'(0) = r$, i.e., stability for $0 < r < 1$ respectively unstable behaviour for $r > 1$. For $\bar{x}_2 = 1 - \frac{1}{r}$ it holds: $f'(1 - \frac{1}{r}) = r - 2r(1 - \frac{1}{r}) = 2 - r$, i.e., it is stable for $1 < r < 3$, yielding different cases:

$$\begin{aligned} r < 1 & \quad \bar{x}_1 = 0 \text{ stable}, \quad \bar{x}_2 = 1 - \frac{1}{r} < 0 \text{ unstable} \\ 1 < r < 2 & : \bar{x}_1 = 0 \text{ unstable}, \bar{x}_2 = 1 - \frac{1}{r} \text{ stable} \\ 2 < r < 3 & : \bar{x}_1 = 0 \text{ unstable}, \bar{x}_2 = 1 - \frac{1}{r} \text{ oscillatory stable} \\ r > 3 & : \quad \bar{x}_1 = 0 \text{ unstable}, \bar{x}_2 = 1 - \frac{1}{r} \text{ unstable} \end{aligned}$$

We consider the graphical iteration for the update-function $f(x) = rx - rx^2$. The graph of this function is a parabola, which is open down-side, intersecting $(0, 0)$ and $(1, 0)$ and with a local maximum at $f'(x) = 0 \Leftrightarrow r - 2rx = 0 \Leftrightarrow x = \frac{1}{2}$, $f(x) = \frac{r}{4}$ (Fig. 2.6). We observe: At $r = 1$ $\bar{x}_1 = 0$ loses its stability (there $f'(0)$ becomes > 1), at the same time another stable stationary point appears. This phenomenon is called “transcritical bifurcation”. Two stationary points (one stable, one unstable) meet and thereby exchange their stability. Generally, an abrupt change of the qualitative behaviour, dependent on parameter values, is called bifurcation.

Next, we consider the case $r > 3$. Assertion: For $r > 3$, there are orbits of period 2 (so-called “oscillations”). These are fixed points of the function $g = f^2$, i.e., they satisfy

$$x_{n+2} = f(x_{n+1}) = x_n \text{ resp. } x_n = f(f(x_n)).$$

Obviously, fixed points of f are also fixed points of g , but not reversely. Therefore, we look for a \bar{x} , such that $\bar{x} = g(\bar{x})$, i.e.,

$$\begin{aligned} \bar{x} &= f(f(\bar{x})) \\ &= rf(\bar{x})(1 - f(\bar{x})) \\ &= r(r\bar{x}(1 - \bar{x}))(1 - r\bar{x}(1 - \bar{x})). \end{aligned}$$

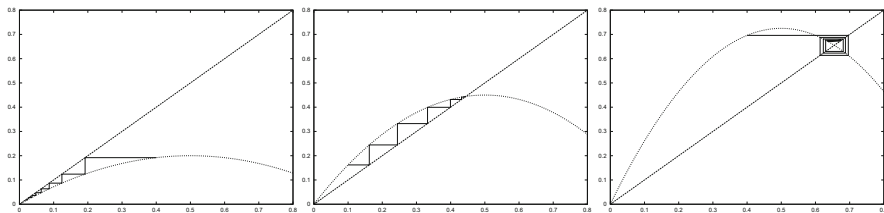


Fig. 2.6 Qualitative behaviour for the discrete logistic equation, cases $0 < r < 1$, $1 < r < 2$, $2 < r < 3$ (from left to right)

This equation can be solved for \bar{x} . Except for the already known stationary points $\bar{x}_1 = 0$ and $\bar{x}_2 = 1 - \frac{1}{r}$ we obtain

$$\bar{x}_{3,4} = \frac{-(r^3 + r^2) \pm \sqrt{(r^3 + r^2)^2 - 4(-r^3)(-r^2 - r)}}{-2r^3}.$$

$\bar{x}_{3,4}$ are real for $r > 3$ and have the following property:

$$f(\bar{x}_3) = \bar{x}_4 \text{ and } f(\bar{x}_4) = \bar{x}_3.$$

The stability of the periodic orbit of f is equivalent to the stability of the fixed point of g , hence, we consider

$$\begin{aligned} g'(\bar{x}_3) &= [f(f(\bar{x}_3))] = f'(f(\bar{x}_3)) \cdot f'(\bar{x}_3) = f'(\bar{x}_4) \cdot f'(\bar{x}_3) \\ g'(\bar{x}_4) &= f'(\bar{x}_3) \cdot f'(\bar{x}_4). \end{aligned}$$

As $f'(x) = r - 2rx$ we find

$$\begin{aligned} g'(\bar{x}_3) &= (r - 2r\bar{x}_4)(r - 2r\bar{x}_3) \\ &= r^2(1 - 2\bar{x}_3 - 2\bar{x}_4 + 4\bar{x}_3\bar{x}_4). \end{aligned}$$

The result is:

$$\begin{array}{ll} \text{For } r > 3, r \text{ "near" } 3: & |g'(\bar{x}_3)| < 1 \Rightarrow \text{stable} \\ r = 1 + \sqrt{6} & g'(\bar{x}_3) = -1 \Rightarrow \text{Stability is lost} \end{array}$$

For more details and special cases, see [58].

For larger r (> 3) there happens so-called period-doubling (which can be computed analogously, e.g. by $h(x) = g(g(x)) = f(f(f(x))) \dots$). It can be shown that in each case the orbit with the larger period is stable (Feigenbaum). There are also orbits with other periods. It was shown by Smale and Williams that the discrete logistic equation has an orbit of minimal period 3 for $r = 3.83$. Hence, the assumptions of the Theorem of Li and Yorke are fulfilled for this equation, i.e., the discrete logistic equation possesses periodic orbits of all periods.

By examining the equation for parameter values near $r = 3.83$, the following behaviour is found: In the parameter interval $[1, 4]$, there is a kind of “window” (α, β) (which is approximately $\alpha = 3.82$, $\beta = 3.84$) such that for all $r \in (\alpha, \beta)$ there exist a stable and an unstable orbit of period 3. At the lower end of this parameter interval, these two orbits appear by a saddle-node-bifurcation; at the upper end, the stable one shows a period doubling, creating a stable orbit of period 6.

The qualitative behaviour can be represented by a so-called bifurcation diagram. In each case, the “stable objects” will be plotted (Fig. 2.7). Creating such a diagram with the aid of a computer can be done as follows:

- Choose a parameter value (here it is done for r)
- Run 1,000 steps of iteration (from an arbitrary starting value).

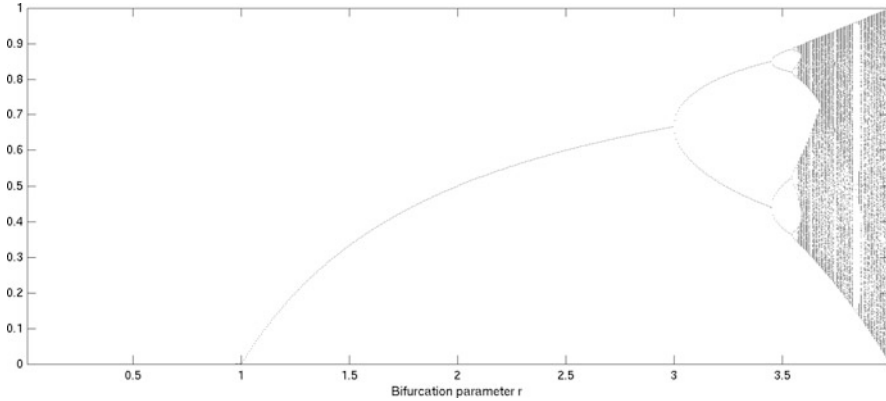


Fig. 2.7 Bifurcation diagram for the discrete logistic equation, bifurcation parameter r ; behaviour for $0 < r < 4$

- Plot the next 1,000 values (of the iteration) in the line above the chosen r .
- Do the same procedure for other values of r

The discrete logistic equation, although it looks so simple, exhibits chaotic behaviour for “large” values of r . This means that e.g. for slightly altered starting conditions, it will show a quite different time course, may look like “jumping”, unpredictable.

This chaotic behaviour is not caused by stochastic or random influences, it can be exactly reproduced by starting under the same conditions, as we consider here a deterministic model.

How realistic is such a chaotic behaviour, does this appear in real-world ecological systems or is this a more or less artificial finding? In reality, it is difficult to decide which influences are caused by a “deterministic chaotic behaviour” and which ones are due to stochastic influences.

The logistic equation is a nice example for a nonlinear difference equation with a parameter that influences the behaviour of the system extensively. In biological applications it is used not so often, it is more a useful “pedagogical” example. But the results and methods can be used everywhere. There are other, more realistic models, which describe the limited growth of a population. Further information about the discrete logistic equation can be found e.g. in [43, 58, 91, 123, 180].

2.1.2.5 Alternative Discrete Population Models

As the discrete logistic equation has some disadvantages (e.g. positivity may be lost or “too chaotic” behaviour, as a consequence of overcompensation), many alternative discrete population models were introduced. We only mention a few examples here; some more information can be found e.g. in [152]. The basic idea is

always to start off with a linear growth model, $x_{n+1} = rx_n$. Next the observation that competition decreases the surviving offspring is included: There is a monotonously decreasing function depending on the population size $g(x)$ that indicates the fraction of newborn that reach the reproductive age. All in all, we have $x_{n+1} = rg(x_n)x_n$. The function $g(x)$ now is chosen in different ways to emphasise certain aspects of the population dynamics.

The model of Varley, Gradwell and Hassell [225] uses $g(x) = 1/(\alpha x^b)$, $\alpha > 0$,

$$x_{n+1} = \frac{r}{\alpha} x_n^{1-b}.$$

The function $g(x)$ is monotonously decreasing, and the resulting model assumes a mathematically simple form. However, the draw-back of this model is that $g(x)$ possesses a pole at $x = 0$. To overcome this difficulty, Hassell [111] adapted the survival-function $g(x) = (1 + \alpha x)^{-b}$ and arrived at:

$$x_{n+1} = rx_n(1 + \alpha x_n)^{-b}.$$

As $g(0) = 1$, we are now able to interpret $g(x)$ as the surviving fraction of newborns. In contrast to the logistic equation, this model preserves positivity. In this, it is quite satisfying. However, a rational function is rather nasty to deal with. If we define $\alpha = 1/(iK)$, $b = i$ and let i tend to infinity, we find an exponential function, $(1 + x/(iK))^{-i} \rightarrow \exp(-x/K)$. As mathematicians love exponential functions this model (known as the Ricker model) is often used,

$$x_{n+1} = r x_n e^{-x_n/K}. \quad (2.2)$$

The Ricker model is well-suited for the description of fish or insect population dynamics, and is also called “spawner-recruit curve” as it relates the present spawning stock to the recruits (the new fish). Apart of its rather mathematical derivation, it can be also evidenced by biological arguments (see e.g. [164]): Consider spawning fish. Each fish produce r offspring. If we have x_n spawners in generation n , we have rx_n offspring. These individuals compete until they become adults. In our idea of the world, this competition is very simple: each individual fights with each other individual. The one who wins all these fights will be able to reproduce again. The probability to win one interaction is p . As each individual has to go through rx_n interactions, the probability to be successful in all interaction reads

$$p^{rx_n} = e^{r \ln(p)x_n} = e^{-x_n/K}$$

where $K = -1/(r \ln(p)) > 0$. Advantage of this formulation is e.g. the interpretation of K as a carrying capacity. Figure 2.8 shows the bifurcation diagram for the Ricker model, with bifurcation parameter r , and fixed $K = 1$.

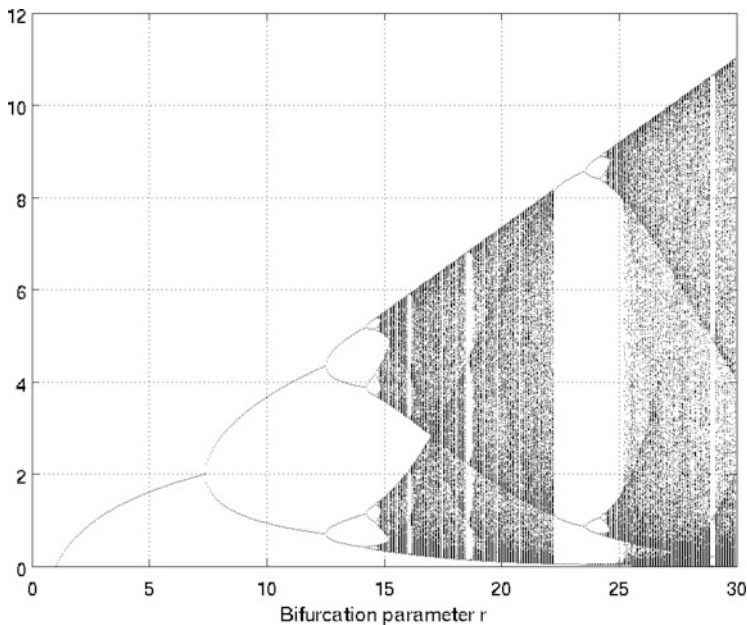


Fig. 2.8 Bifurcation diagram for the Ricker equation

In [15] wasps (*Vespula vulgaris*) have been investigated. These wasps have been brought to New Zealand and form a threat for some bird and insect species. The authors measured for five consecutive years the number of wasp populations per hectare at five different locations. The data for one of the locations (that we use here) reads 10.5, 15.8, 8.2, 11.6, and 12.1 wasp populations per ha. The authors propose to use a Ricker model, and estimate the parameters. Thereto they note that

$$\ln(x_{n+1}/x_n) = \ln(r) - x_n/K.$$

After a suitable transformation of the data, a linear regression can be used to determine the parameters (see Fig. 2.9a). We find $r = 5.4$ and $K = 5.7$ populations/ha. The pseudo-phaseplane plot, where we plot x_{n+1} over x_n , is presented in Fig. 2.9b together with the r.h.s. of the Ricker model. We find that the data x_n behave roughly as the function estimated. However, the time series is rather short, and the data are noisy for sure. Especially weather will influence the dynamics crucially, and we cannot expect to obtain a perfect agreement of theory and data.

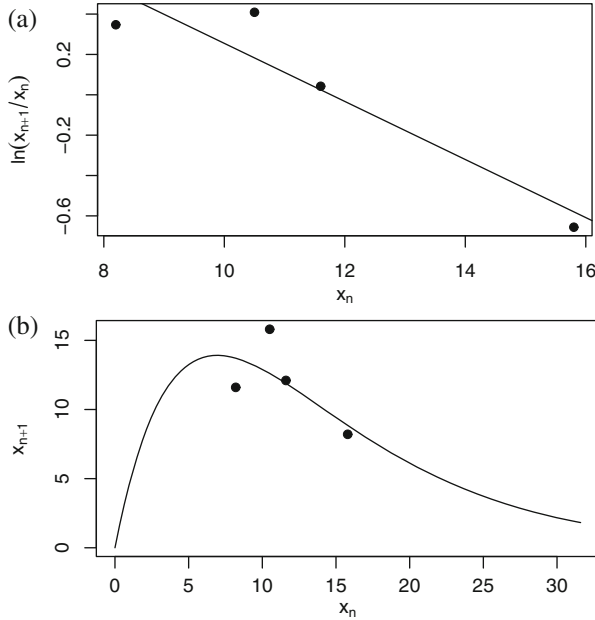


Fig. 2.9 (a) Linear regression to estimate the parameters of the Ricker model for the wasp population (see text). (b) The r.h.s. of the Ricker model with the parameters estimated. *Bullets*: data points

2.1.2.6 Stability of Stationary Points in the Continuous Case

First, we want to clarify the often-used term “stable equilibrium” of an ODE of the form $\frac{dx}{dt} = f(x)$. The ideas in the present section parallel the considerations in Sect. 2.1.2.4, where we performed the stability analysis for the discrete logistic equation. Let \bar{x} be a stationary point, i.e., $f(\bar{x}) = 0$.

Definition 2.7 (Stability of a stationary point) A stationary point \bar{x} is called stable if for all $\varepsilon > 0$ there exists a $\delta > 0$ in such a way that for all $x(t_0) = x_0$ with $|x_0 - \bar{x}| < \delta$ it is $|x(t) - \bar{x}| < \varepsilon$ for all $t > t_0$.

This means, stability only says that a solution will stay nearby the stationary point if starting close to it. Only an asymptotically stable stationary point guarantees that the solutions, starting sufficiently close to the stationary point, will really tend to it:

Definition 2.8 (Asymptotic stability of a stationary point) A stationary point \bar{x} is called asymptotically stable if it is stable and if there is a $\delta_0 > 0$ such that for all x_0 satisfying $|x_0 - \bar{x}| < \delta_0$ it is

$$\lim_{t \rightarrow \infty} |x(t) - \bar{x}| = 0.$$

We still miss a practical criterion how to determine stability of a given stationary point. For that purpose, we can again use the trick of linearisation, as already done for the discrete case:

Theorem 2.9 *Let \bar{x} be a stationary point, $f(x)$ a continuously differentiable, scalar function. Let $f'(\bar{x}) \neq 0$. If $f'(\bar{x}) < 0$, then \bar{x} is asymptotically stable; if $f'(\bar{x}) > 0$, then it is unstable.*

Proof Again, we use Taylor expansion around the stationary point \bar{x} . Let $z(t) = x(t) - \bar{x}$, so we get

$$\frac{dz}{dt} = f(\bar{x}) + f'(\bar{x})z + g(z).$$

$g(z)$ contains the higher order terms, so for a small δ neighbourhood around 0 it is at least $g(z) \leq \varepsilon|z|$. Due to the fact that \bar{x} is a stationary point, this equation reduces to

$$\frac{dz}{dt} = f'(\bar{x})z + g(z).$$

Since we consider a scalar, autonomous differential equation, z' never changes sign Fig. 2.10. Furthermore, $g(z) = o(|z|)$ implies that $f'(\bar{x}) + g(z)$ carries the sign of $f'(\bar{x})$ if z is small enough and $f'(\bar{x}) \neq 0$. We are faced with two cases:

- (1) $f'(\bar{x}) < 0$. Then, $|z(t)|$ is decreasing if $z(0)$ is small enough. Since $f(\bar{x}) + g(z)$ is uniformly bounded away from zero for $|z| < z_0$ and z_0 small enough, $z(t)$ tends exponentially fast to zero, indicating that \bar{x} is locally asymptotically stable.
- (2) The second case, $f'(\bar{x}) > 0$, implies that $|z(t)|$ grows (if $z(0)$ is small enough), and hence in that case \bar{x} is unstable. \square

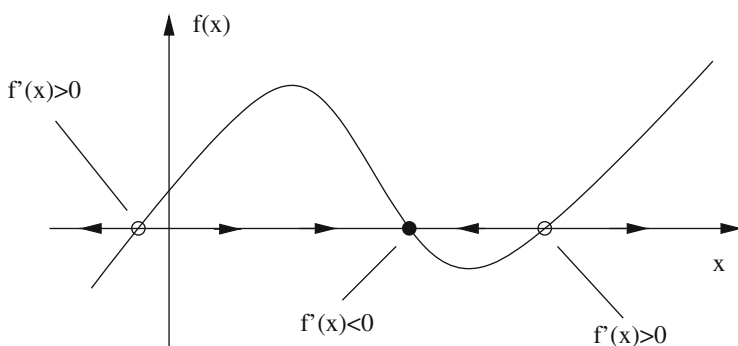


Fig. 2.10 Stability of the stationary points of $\dot{x} = f(x)$. On the y-axis $f(x)$ is indicated. The arrows on the x-axis point in the direction the solution moves to (to the left if $f(x) < 0$, to the right if $f(x) > 0$). The zeros of f are stationary points; open circles indicate unstable, bullets stable stationary points

Remark 2.10

- (a) We emphasise that no statement is made by the theorem if $f'(\bar{x}) = 0$; linearisation is not suitable tool in that case, as the higher order terms play here an important role.
- (b) The solution of an autonomous ODE in one dimension is necessarily monotone: in-between two neighbouring zeros, a function $f(x)$ is either strictly positive or strictly negative. Thus, the solution $x(t)$ of $\dot{x} = f(x)$ will be either monotonously decreasing or increasing until it hits the next stationary point. Theorem 2.9 can be viewed as a direct consequence of this observation (see Fig. 2.10).

2.1.2.7 Continuous Logistic Growth

Let us return to the description of population growth. We include a limitation of growth into the model, but now in a continuous time model. Such a model was introduced by Verhulst by the following assumptions:

- A biotope has a carrying capacity $K(t)$, where $K(t) > 0$ is a continuous function
- For small densities of populations, there is approximately exponential growth with an exponent $a(t)$, where $a(t) > 0$ is continuous.
- The increase \dot{x} of the population density x is additionally proportional to the remaining living space $((K - x)$ resp. $(1 - \frac{x}{K}))$.

This leads to the following equation:

$$\dot{x}(t) = a(t)x(t) \left(1 - \frac{x(t)}{K(t)}\right). \quad (2.3)$$

Solving the time-dependent Verhulst equation can easily be done by the so-called “trick of Riccati”: We introduce a new variable $v(t) = \frac{1}{x(t)}$. Without loss of generality let $t_0 = 0$, $v_0 = \frac{1}{x_0}$. Hence we get:

$$\begin{aligned} \dot{v}(t) &= -\frac{\dot{x}(t)}{x^2(t)} = -\frac{a(t)x(t)(1 - \frac{x(t)}{K(t)})}{x^2(t)} \\ &= -a(t) \left(\frac{1}{x(t)} - \frac{1}{K(t)}\right) \\ &= -a(t)v(t) + \frac{a(t)}{K(t)}. \end{aligned}$$

Applying variation of constants yields

$$v(t) = v_0 e^{-A(t)} + \int_0^t e^{-(A(t)-A(s))} \frac{a(s)}{K(s)} ds,$$

where $A(t) = \int_0^t a(\tau) d\tau$. We return to the variable $x(t) = \frac{1}{v(t)}$ and get

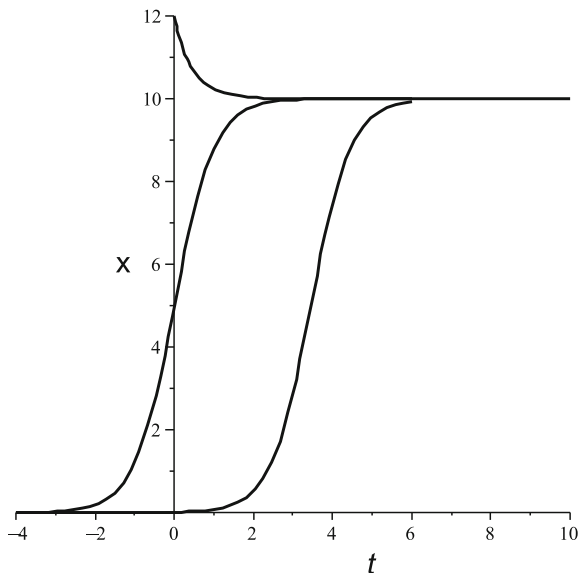
$$x(t) = \frac{x_0}{e^{-A(t)} + u_0 \int_0^t e^{-(A(t)-A(s))} \frac{a(s)}{K(s)} ds}. \quad (2.4)$$

For the special case $a, K = \text{const}$ the explicit solution of the time-independent Verhulst equation reads:

$$\begin{aligned} x(t) &= \frac{x_0}{e^{-at} + x_0 \frac{a}{K} e^{-at} \int_0^t e^{as} ds} \\ &= \frac{x_0}{e^{-at} + \frac{x_0}{K} (1 - e^{-at})} = \frac{x_0}{e^{-at} (1 - \frac{x_0}{K}) + \frac{x_0}{K}} = \frac{x_0 K}{e^{-at} (K - x_0) + x_0}. \end{aligned}$$

The stationary solutions can be seen directly from Eq. (2.3): either $\bar{x} = 0$ (no population at all) or $\bar{x} = K$ (the population assumes the carrying capacity of the system) (Fig. 2.11). For the examination of their behaviour, concerning stability, we can use a fast “graphical trick”. The time-independent Verhulst equation can be written in the form of $\dot{x} = f(x) = ax - bx^2$, where $b = a/K$. In Fig. 2.12, the right-hand side of the differential equation is plotted against u . The roots of $f(x)$ correspond to the stationary points; in case of $f(x)$ positive \dot{x} is positive, i.e., the arrow points to the right and the population is growing; in case of $f(x)$ negative \dot{x} is negative, i.e., the arrow points to the left and the population is decreasing. Hence we get: Let \bar{x} a stationary point.

Fig. 2.11 Time course of typical solution of the Verhulst equation: The chosen parameter values are $a = 2$ and $K = 10$, using different initial values. Starting above the carrying capacity yields a monotone decreasing solution, starting below the carrying capacity (but >0) yields a S-shaped monotone increasing solution. The figure was plotted using OCTAVE, the code can be found in the appendix



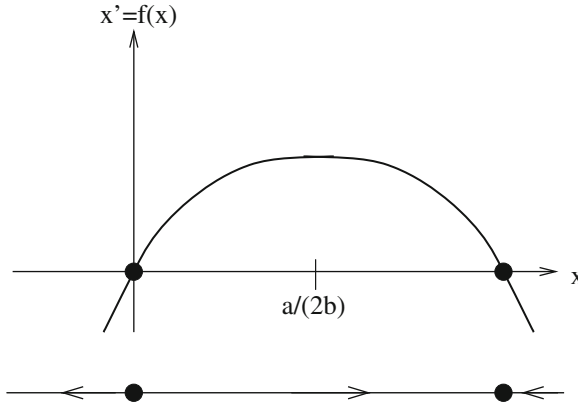


Fig. 2.12 Graph of the right-hand side function of the ODE (Verhulst model) against x

$$f'(\bar{x}) < 0: \quad \bar{x} \text{ stable stationary point}$$

$$f'(\bar{x}) > 0: \quad \bar{x} \text{ unstable stationary point.}$$

An interesting special case concerns parameters in the form of periodic functions with period T . Typical reasons for that may be seasonal effects which influence birth rate and carrying capacity. Assume the period to be $T = 1$, hence

$$a(t + 1) = a(t), \quad K(t + 1) = K(t).$$

A solution with period 1 and initial value x_0 satisfies $x_1 = x(1) = x(0) = x_0$. By formula (2.4) we get

$$x_1 = \frac{x_0}{e^{-\int_0^1 a(s) ds} + x_0 \int_0^1 e^{-\int_s^1 a(\tau) d\tau} \frac{a(s)}{K(s)} ds} \quad (2.5)$$

which leads to

$$x_0 = \frac{1 - e^{\int_0^1 a(s) ds}}{\int_0^1 e^{-\int_s^1 a(\tau) d\tau} \frac{a(s)}{K(s)} ds}.$$

For the Verhulst equation with periodic parameters, there is exactly one periodic solution (except for $x = 0$). The right hand side of (2.5) defines a function $g : \mathbb{R} \rightarrow \mathbb{R}$ with $g(x_0) = x_1$ which has the following properties: $g(0) = 0$, $g(x_0) < x_0$ for large x_0 , g is strictly monotone increasing and concave. Hence, all solutions with initial data $x_0 > 0$ converge towards the unique non-trivial periodic solution.

In the special case of a constant a the periodic solution reads

$$x(t) = \frac{x_0}{e^{-at} + x_0 \int_0^t e^{-a(t-s)} \frac{1}{K(s)} ds}$$

with the initial value

$$x_0 = \frac{1 - e^a}{a \int_0^1 e^{-a(1-s)} \frac{1}{K(s)} ds}.$$

Using this expression for u_0 , we get after several steps

$$x(t) = \left(\frac{\int_0^1 e^{-a(1-s)} \frac{1}{K(s)} ds}{\int_0^1 e^{-a(1-s)} ds} e^{-at} + \frac{\int_0^t e^{-a(t-s)} \frac{1}{K(s)} ds}{\int_0^t e^{-a(t-s)} ds} (1 - e^{-at}) \right)^{-1}.$$

Two extreme cases can help to understand the underlying behaviour:

The limit $a \rightarrow \infty$ yields

$$x(t) = K(t).$$

That means: For a (the growth rate) large, the population adapts fast to the changes of the capacity.

For $a \rightarrow 0$ (slow population growth) the limit reads

$$x(t) = \left(\int_0^1 \frac{1}{K(s)} ds \right)^{-1}.$$

If the population can adapt only slowly, it stays nearly constant, at a value of the harmonic mean value of the capacity.

2.1.2.8 Non-dimensionalisation and Reparametrisation

When dealing with realistic models, the variables and parameters of the model have dimensions which are absolutely important for quantitative statements. In the example of the Verhulst equation, $u(t)$ might have the dimension “number of animals in the systems”, or “population density” which corresponds to “number of animals per area”. If the system is to solve numerically, one has to get rid of units. The system is to non-dimensionalise. If one aims at an analytical treatment of the model, it is often useful to reparametrise the system: it is possible to choose other units (hours instead of seconds, say), and in using this degree of freedom to reduce the number of free parameters. Within this process, it is also a good idea to select a natural scale for state variables and parameters. As a consequence, time scales are revealed that may help to simplify the system further (see e.g. Michaelis-Menten kinetics, Sect. 5.1.3).

Non-dimensionalisation In order to clarify how to non-dimensionalise a model, let us consider the Verhulst equation $x' = ax(1 - x/K)$, $x(0) = x_0$ for a bacterial

community. Typically, every symbol comes with its own units, e.g.

$$[x_0], [x], [K] = \text{cells/l}, \quad [t] = h, \quad [a] = 1/h.$$

E.g., K is given as $K = k \text{ cells/l}$, where k is only a real number. Similarly $x_0 = y_0 \text{ cells/l}$, $t = \tau h$, $a = \alpha/h$. Slightly more involving is $x(t)$; here, we have $x(t)$ given by

$$x(t) = y(t/h) \text{ cells/l} = y(\tau) \text{ cells/l}.$$

$x(t)$ is represented by the real-valued function $y(\tau)$ which also takes the real numbers as argument. Now, how can we transform the Verhulst equation into an ODE consisting of real numbers only? The initial condition is simple:

$$x(0) = y(0/h) \text{ cells/l} = x_0 = y_0 \text{ cells/l} \quad \Rightarrow \quad y(0) = y_0.$$

In a similar manner, we find

$$\begin{aligned} \frac{dx(t)}{dt} &= \frac{dy(\tau) \text{ cells/l}}{d\tau h} = ax(1 - x/K) = (\alpha/h)y(\tau) \text{ cells/l}(1 - y/k) \\ \Rightarrow \quad y'(\tau) &= \alpha y(1 - y/k). \end{aligned}$$

Units always have to cancel out. As trivial as this finding might seem to be, for more complex models that is a good check for consistency.

It is also possible to use different units. We can assume that a is not given per hours but per seconds, $a = \tilde{\alpha}/s$. The same procedure as above yields (with the additional information that $h = 3,600 \text{ s}$)

$$y'(\tau) = 3,600 \tilde{\alpha} y(1 - y/k).$$

Numerical constants are appearing in the equation. If we use the natural scales for all parameter and state variables, these numerical constants indicate which processes are fast and which are slow. In this example, we conclude that we missed to use the natural scale for time: instead of h we should have used s , as this removes the rather large numerical constant 3,600 again from the equation. However, in more complex systems it will turn out that different processes “live” on different time scales. We will learn later how to deal with such a situation. The discussion of the “natural” scales is already close to reparametrisation, which we consider next.

Reparametrisation The aim of reparametrisation is slightly different than that of non-dimensionalisation. Here, we aim to use the freedom to choose units in order to get rid of as many parameters as possible; at the same time, it is possible to introduce time scales in choosing natural dimensions for parameters and state variables. Therefore, we do not need to be too concrete in the statement of units. For any state variable, we introduce an own scale, i.e., in case of the Verhulst model

$$t = \hat{t} \tau, \quad x = \hat{x} y.$$

In principle, also more complex transformations are possible, e.g. $t = \hat{t}\tau + \hat{t}_1\tau^2$ or $t = \hat{t}\tau + \hat{t}_2$, but practical experience shows that the linear approach is the most powerful. The constants (scales) \hat{t} and \hat{x} can be arbitrarily chosen (as long as they are non-zero). We are left with a system with new independent variables τ and y and (this is the trick!) two new free parameters in the model equations – the constants \hat{t} and \hat{x} . These free constants can be used to do several things: (a) we could simply do a non-dimensionalisation in defining $\hat{x} = \text{cells/l}$ and $\hat{t} = \text{h}$. This, however is not the main goal of reparametrisation as we will find in a minute. (b) We can introduce typical scales (time scales, length scales or whatever scales are in the system). And indeed, similar to the non-dimensionalisation, often knowledge about the natural scales of the different processes are included in the choice of the constants. (c) Last, we may simply use these additional, free constants to eliminate as many parameters as possible from the model equations.

Let us now explicitly transform the Verhulst equation using the definitions $t = \hat{t}\tau$ and $x = \hat{t}y$,

$$\begin{aligned}\frac{dx(t)}{dt} &= \frac{d\hat{t}y(\tau)}{d\hat{t}\tau} = \frac{\hat{x}}{\hat{t}} \frac{dy(\tau)}{d\tau} = a\hat{x}y(\tau)[1 - \hat{x}y(\tau)/K] \\ \Leftrightarrow y' &= (\hat{t}a)y(1 - (\hat{x}/K)y).\end{aligned}$$

If our aim (and this is, like discussed above, the primarily aim of re-parametrisation) is to minimise the number of parameters of the model, we clearly choose $\hat{t} = 1/a$ and $\hat{x} = K$, which yields

$$y' = y(1 - y).$$

Of course, it is possible to retransform to the original problem or its solution. However, in practice it is often rather difficult to find back the original scales and e.g. to relate the rescaled model to given data. Non-dimensionalised models are nice to simulate and for parameter fitting, reparametrised models are better suited to investigate the model's behaviour analytically.

In this example, the reparametrisation allows to reduce the population growth models of Verhulst type to problem without any parameter. This will not be the case for all models, especially if they are more complex. Nevertheless, reparametrisation helps to reduce the number of relevant parameters and to identify characteristic parameters.

Note that “rate” and “rate constant” do have different meaning. The rate describes the change of a variable per time unit. If we, e.g., consider the logistic equation, we have $\dot{x} = ax(1 - \frac{x}{K})$. In this case, the change of x per time unit reads $ax(1 - x/K)$. This is the rate. A rate constant, in difference, is a proportionality factor that appears in the rate: mostly, the rate is proportional to a certain function of the state; in the present setup, the rate is proportional to $x(1 - \frac{x}{K})$. The proportionality constant, that is also called rate constant, is a . A rate constant has a determined unit: if the state variable has units N/V , and time has the unit T , the rate carries the unit $(N/V)/T$

(change of state per time). The rate constant converts the unit of the state into the unit of the rate, i.e., carries the unit $1/T$.

In theoretical biology, often the terminus “rate” is used instead of “rate constant”, also in this book, neglecting the correct meaning. So, one has to be careful if really a rate is meant or, being more precise, a rate constant.

2.1.2.9 Branching Process

Until now we basically considered large populations. In the present section, we aim to understand the new effects coming in if small populations are considered. From the linear models, we already know what to expect: we need to take into account stochasticity, and we expect that a population may die out in finite time. We only consider the time-continuous case; it is straightforward to work out the similar arguments in the time-discrete case.

The Model

The idea of the logistic model is the competition for resources. Hence, the birth rate is decreased, and the death rate increased by the population size. For simplicity, we only look at the decrease in the birth rate and assume that the death rate is independent of the population size.

State: Let X_t = number of individuals at time t .

Dynamics: There are two processes, birth and death:

- Birth rate: $b(X_t) = \beta(1 - X_t/N)$, $N \in \mathbb{N}$, i.e.,

$$P(X_{t+\Delta t} = X_t + 1) = \beta(1 - X_t/N)X_t\Delta t + o(\Delta t).$$

- Death rate: $\mu(X_t) = \mu$, i.e.,

$$P(X_{t+\Delta t} = X_t - 1) = \mu X_t\Delta t + o(\Delta t).$$

The population size cannot exceed the maximal population size N , since for $X_t = N$ we find $b(X_t) = 0$. From this fact it is possible to conclude that the population dies out with probability one (see Exercise 2.4). E.g. all species living on earth certainly do have a finite carrying capacity, i.e., the population size is bounded. Thus, every species on earth has to die out, but this is not what we observe. This apparent contradiction is one of the interesting issues that have to be clarified.

Analysis I: Large Population Size

In order to analyse this process, one may scale it in certain (different) ways. We let always $N \rightarrow \infty$ (s.t. the nonlinearity becomes weaker and weaker). At the same time, one may rescale time resp. bound the time in a certain way. The scaling of the time is crucial for the result.

If $N \rightarrow \infty$, we may scale the process such that we derive an ODE. Let $Z_t = X_t/N$, then

$$P(Z_{t+\Delta t} = Z_t + 1/N) = \beta(1 - Z_t)Z_t N \Delta t + o(\Delta t)$$

$$P(Z_{t+\Delta t} = Z_t - 1/N) = \mu Z_t N \Delta t + o(\Delta t)$$

Let $z(t) = E(Z_t)$. We obtain the ODE in our usual, heuristic manner,

$$\begin{aligned} \frac{E(Z_{t+\Delta t} | Z_t) - Z_t}{\Delta t} &= \beta(1 - Z_t)Z_t N - \mu Z_t N \\ &\downarrow \quad \Delta t \rightarrow 0 \\ \dot{z} &= N[\beta(1 - z)z - \mu z], \end{aligned}$$

where we approximated $E(Z_t^2) \approx E(Z_t)^2$. Why is this possible?

Recall that $Z_t = X_t/N$. Now,

$$\begin{aligned} E(Z_t^2) &= E((Z_t - z(t) + z(t))^2) = E((Z_t - z(t))^2) + z^2(t) + \underbrace{2E((Z_t - z(t))z(t))}_{=0} \\ &= z^2(t) + E((X_t - E(X_t))^2)/N^2 \\ &= z^2(t) + \text{Var}(X_t)/N^2 \end{aligned}$$

Heuristically, X_t counts individuals. The variance structure should be thus similar to the Poisson distribution, i.e., proportional to X_t . As $X_t \leq N$, we have $\text{Var}(X_t) = \mathcal{O}(N)$ and hence

$$E(Z_t^2) = z^2(t) + \mathcal{O}(1/N)$$

s.t. $E(Z_t^2) \approx z^2(t)$ for large N . Let us return to the ODE. By rescaling time $t = \tau/N$, we find

$$\dot{z} = -\mu z + \beta(1 - z)z,$$

i.e., the scaled process approaches the deterministic logistic equation. The proof can be found in the work by Kurtz [154].

Analysis II: Linearisation

For the second scaling we let again $N \rightarrow \infty$, but – at the same time – bound the time. In this way, one derives a similar structure like the linearisation at stationary points for nonlinear ordinary differential equations: Though the equation is nonlinear, under certain conditions (all eigenvalues of the linearisation have non-vanishing real part), the dynamics of the linearised equations is locally conjugated (i.e., locally equivalent) to the dynamics of the nonlinear system (Theorem of Hartman-Grobman [98], will be introduced later in Sect. 2.3.1). We are able to prove a similar theorem for the stochastic system. The basic idea of the present section follows Ball and Donnelly [13]; however, we strongly simplify the proof and derive a weaker result.

For the construction of the linear and the logistic birth-death process (coupling of the processes), let (Ω, \mathcal{F}, P) be a random space. Consider two stochastic processes, defined simultaneously on this random space:

(1) Linear Birth-Death Process:

Let $Y_t(\omega)$, $\omega \in \Omega$, denote the population size of a realisation of the linear birth-death process with birth rate β (independent of the population size) and death rate μ .

(2) Logistic Birth-Death Process:

We construct the population size X_t of the logistic birth-death process in the following way: apart from living individuals we define a population of ghosts with population size Z_t . X_t and Z_t are random variables that are defined on the same random space (Ω, \mathcal{F}, P) , and thus we are able to relate single realisations $(X_t(\omega), Z_t(\omega))$ to $Y_t(\omega)$ s.t.

$$Y_t(\omega) = Z_t(\omega) + X_t(\omega).$$

Birth:

- Every individual (Ghost or living individual) of the logistic process has the constant birth rate β (independent of the population size).
- A newborn becomes with probability X_t/N a ghost.
- Children of a ghost are again ghosts.

Death:

- All individuals (“normal individuals” or ghosts) die with the same death rate μ .

In a certain sense, the logistic process describes the linear birth-death process, where the individuals get one more attribute: they are either “normal individuals” or “ghosts”. If we add the “normals” and the ghosts, we obtain the linear process. If we only consider the “normals”, we obtain the logistic process. Both processes agree until $Z_t(\omega) \neq 0$. We are now ready to prove the “linearisation” result.

Theorem 2.11 *Let $X_0 = 1$.*

(a) *If $\beta_0/\mu_0 < 1$, then*

$$P(Z_t = 0) = 1 \quad \text{for } N \rightarrow \infty, \quad t \in \mathbb{R}_+.$$

(b) *If $\beta_0/\mu_0 > 1$, then for all $T \in \mathbb{R}_+$, we find*

$$P(Z_t = 0) = 1 \quad \text{for } N \rightarrow \infty, \quad t \in [0, T].$$

Proof

Step 1: Estimation of the number of birth events

If we are in case (a), we know from Chap. 1, Proposition 1.4, that the population dies out with probability one. Hence, there is for every realisation a stopping time $T(\omega)$, for that $Y_{T(\omega)}(\omega) = 0$. This stopping time is well behaved in that it has a finite expectation.

For $\omega \in \Omega$, let $I = [0, T(\omega)]$ in case (a) and $I = [0, T]$ in case (b). Then define

$$\hat{N}(\omega) = \sup_{t \in I} Y_t(\omega),$$

and

$$\hat{B}(\omega) = \text{total number of birth events in } I \text{ of the linear process.}$$

We find $\hat{N}(\omega) \leq \hat{B}(\omega) + 1$. If we are in case (b), we may estimate the number of birth events by a pure birth process ($\mu = 0$) with birth rate β . The generating function of the population size in such a case is given by (see Chap. 1, Proposition 1.3),

$$f(s, t) = \frac{-\beta s e^{\beta t}}{\beta(s-1) - (\beta s) e^{\beta t}}.$$

i.e., $\tilde{p}_i = P(i \text{ individuals at time } T) \rightarrow 0$ for $i \rightarrow \infty$. Thus,

$$|\{\omega \in \Omega \mid \hat{B}(\omega) \text{ is not finite}\}| \leq \lim_{i \rightarrow \infty} p_i = 0.$$

In case (a) the argument is similar, using the random stopping time $T(\omega)$ instead of the fixed, deterministic time T .

Step 2: X_t and Y_t agree for $N \rightarrow \infty$.

The probability of creating a ghost in a birth event at time t is

$$\begin{aligned} P(\text{creation of a ghost at time } t \mid \text{given a birth event at this time}) &= X_t/N \\ &\leq \hat{N}/N. \end{aligned}$$

The probability of not creating a ghost in a birth event taking place at time t reads

$$P(\text{no creation of a ghost at time } t \mid \text{given a birth event at this time}) \geq 1 - \frac{\hat{N}}{N}.$$

The probability of creating no ghost at all in \hat{B} birth events thus reads

$$P(\text{no ghost at all}) \geq (1 - \hat{N}/N)^{\hat{B}} \rightarrow 1 \quad \text{for } N \rightarrow \infty.$$

Thus,

$$|\{\omega \in \Omega \mid \lim_{N \rightarrow \infty} Z_t(\omega) \neq 0 \text{ a.s. for } t \in I\}| = 0.$$

□

Remark 2.12 Ball and Donnelly are able to prove in the case $\beta_0/\mu_0 > 1$ that

$$Z_t = 0 \quad \text{a.s. for } t \leq C \log(N)$$

where C has to be chosen in an appropriate way.

This is a first, partial answer to the problem that the population dies out for $N < \infty$ a.s.: If $\beta/\mu > 1$, the population is able to spread (without competition), while for $\beta/\mu < 1$, the population will die out anyway even if $N \rightarrow \infty$. However, in order to get an better idea of the two different cases (β/μ larger resp. smaller one) without taking the limit $N \rightarrow \infty$, we consider in the next step ideas about the time to extinction.

Analysis III: Quasi-steady State

For the deterministic logistic equation, one obtains a nontrivial equilibrium (i.e., an equilibrium where the population is not extinct) if $\beta/\mu > 1$. This is not the case for the logistic birth-death process, since we know that the population dies out for sure (Exercise 2.4). However, if $\beta \gg \mu$, we will (e.g. in a simulation) never find that the population dies out. In order to solve this seemingly contradiction, one considers the logistic process X_t under the condition that the process does not die out $\hat{X}_t = X_t | X_t > 0$. In the following we present some results due to Nasell [183].

Definition 2.13 The quasi-steady state of the logistic process is the asymptotic distribution (the Yaglom limit) of the random variable $\hat{X}_t = X_t | X_t > 0$, i.e., the asymptotic distribution of the logistic process under the condition that it does not die out.

Proposition 2.14 *Let $\beta_i = i\beta(1 - i/N)$, $\mu_i = i\mu$ and*

$$A = \begin{pmatrix} 0 & \mu_1 & 0 & \cdots & 0 \\ 0 & -(\mu_1 + \beta_1) & \mu_2 & \cdots & 0 \\ 0 & \beta_1 & -(\mu_2 + \beta_2) & \cdots & 0 \\ 0 & 0 & \beta_2 & \cdots & 0 \\ \cdots & \cdots & \cdots & \cdots & \cdots \\ 0 & 0 & 0 & \cdots & -\mu_N \end{pmatrix} = \left(\begin{array}{c|ccc} 0 & \mu_1 & 0 & \cdots & 0 \\ \hline 0 & & & & \\ \vdots & & \hat{A} & & \\ 0 & & & & \end{array} \right)$$

The distribution of the quasi-stationary state

$$\hat{q}^* = (\hat{q}_1^*, \dots, \hat{q}_N^*)^T$$

is given by the nonlinear eigenvalue problem

$$\hat{A}\hat{q}^* = -\mu_1\hat{q}_1^*\hat{q}^*.$$

Proof First, we introduce some notations. Let

$$\begin{aligned} q_i(t) &= P(X_t = i), & \hat{q}_i(t) &= P(\hat{X}_t = i) \\ q(t) &= (q_0(t), \dots, q_N(t))^T, & \tilde{q}(t) &= (q_1(t), \dots, q_N(t))^T \\ \hat{q}(t) &= (\hat{q}_1(t), \dots, \hat{q}_N(t))^T. \end{aligned}$$

Then,

$$\dot{q} = Aq.$$

Since $\hat{X}_t = X_t | X_t > 0$, we find for $i = 1, \dots, N$

$$P(\hat{X}_t = i) = \frac{P(X_t = i \text{ and } X_t > 0)}{P(X_t > 0)} = \frac{P(X_t = i)}{1 - P(X_t = 0)}$$

i.e.,

$$\hat{q}(t) = \frac{\tilde{q}(t)}{1 - q_0(t)}.$$

and

$$\begin{aligned} \frac{d}{dt}\hat{q}(t) &= \frac{1}{1 - q_0(t)} \frac{d}{dt}\tilde{q}(t) + \frac{1}{(1 - q_0(t))^2} \tilde{q}(t) \frac{d}{dt}q_0(t) \\ &= \frac{1}{1 - q_0(t)} \hat{A}\tilde{q}(t) + \frac{1}{(1 - q_0(t))^2} \tilde{q}(t)(\mu_1 q_1(t)) \\ &= \hat{A}\hat{q}(t) + \mu_1 \hat{q}_1(t) \hat{q}(t) = (\hat{A} + \mu_1 \hat{q}_1(t)) \hat{q}(t). \end{aligned}$$

The quasi-steady state satisfies $\hat{q}'(t) = 0$, i.e.,

$$(\hat{A} + \mu_1 \hat{q}_1^*) \hat{q}^*(t) = 0.$$

□

Remark 2.15 This nonlinear eigenvalue problem cannot be solved explicitly. However, there are several approximations possible (see [183]). The shape of the quasi-steady state will look completely different for $R_0 = \beta/\mu < 1$ and $R_0 = \beta/\mu \gg 1$ (Fig. 2.13): If $\beta/\mu < 1$, the distribution is monotonously decreasing with \hat{q}_1 is maximal: the trajectories “want” to die out, i.e., jump to population size zero, but are not allowed to. Thus, they are centred at small population sizes. If $\beta/\mu \gg 1$, then the distribution looks approximately normal with the mean given by the population size where birth and death balances,

$$i\mu = i\beta(1 - i/N) \quad \Leftrightarrow \quad i = N(1 - \mu/\beta).$$

Here, the population is naturally in its equilibrium, far away from zero population size. However, natural fluctuations (the normal distribution does have tails that reach

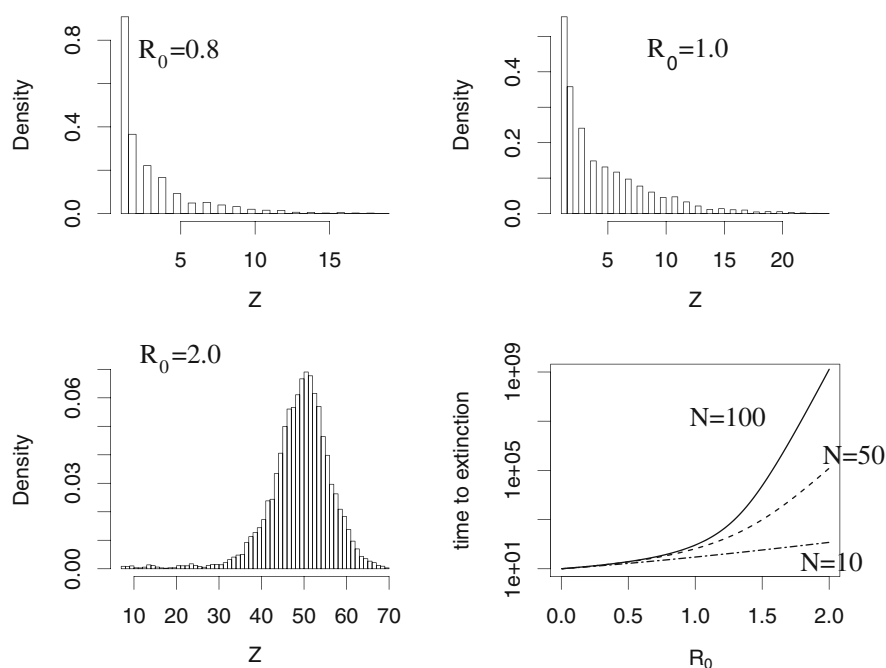


Fig. 2.13 Simulation of the quasi-stationary solution for different values of R_0 (population size 100, $\mu = 0.1$). *Right, bottom:* Expected time to extinction (in logarithmic scale) over R_0 for three different population sizes ($\mu = 0.1$)

to zero population size) will bring a trajectory from time to time (very seldom) close to extinction. In this case, the realisations of the original process $X_t(\omega)$ die out. By this mechanism, realisations eventually have to die out, though they are naturally centred around $N(1 - \mu/\beta)$, far away from zero.

Another idea to characterise the two situations $R_0 = \beta/\mu$ smaller resp. larger one is to consider the expected time to extinction. The time to extinction, however, depends on the initial population size. It is not clear how to handle this dependency. The quasi-stationary state should represent the equilibrium distribution of the logistic process under the condition that it is not extinct yet. It may be a good idea to define “the” time of extinction as the time of extinction if we start in the quasi-steady state. We find a relatively simple expression for the expectation of the time to extinction.

Proposition 2.16 *Consider the logistic process starting in the quasi-stationary distribution \hat{q}^* . The expectation for the time to extinction is given by*

$$E(\text{time to extinction if } q(0) = (0, \hat{q}^*)^T) = 1/(\mu_1 \hat{q}_1^*).$$

Proof We solve (with the nomenclature of the proof of the Theorem before)

$$\dot{q} = Aq, \quad q(0) = (0, \hat{q}^*)^T.$$

Thus,

$$\begin{aligned} \frac{d}{dt} q_0 &= \mu_1 \tilde{q}_1(t) \\ \frac{d}{dt} \tilde{q} &= \hat{A} \tilde{q}(t) \end{aligned}$$

Since $\tilde{q}(0) = \hat{q}^*$ is an eigenvector of \hat{A} , we find at once $\tilde{q}(t) = e^{-\mu_1 \hat{q}_1^* t} \hat{q}^*$. Thus

$$q_0(t) = \int_0^t \mu_1 (e^{-\mu_1 \hat{q}_1^* t} \hat{q}_1^*) dt = 1 - e^{-\mu_1 \hat{q}_1^* t}.$$

The expectation for the time to extinction now reads (where we used partial integration in the first step).

$$\begin{aligned} E(\text{time to extinction}) &= \int_0^\infty t \left(-\frac{d}{dt} P(\text{alive at time } t) \right) dt \\ &= \int_0^\infty (1 - q_0(t)) dt = \int_0^\infty e^{-\mu_1 \hat{q}_1^* t} dt = 1/(\mu_1 \hat{q}_1^*). \end{aligned}$$

□

As $\mu_1 \hat{q}_1^*$ is just the Perron eigenvalue of \hat{A} , we may rewrite the last proposition as

$$\text{Time to extinction} = 1/\rho(\hat{A}).$$

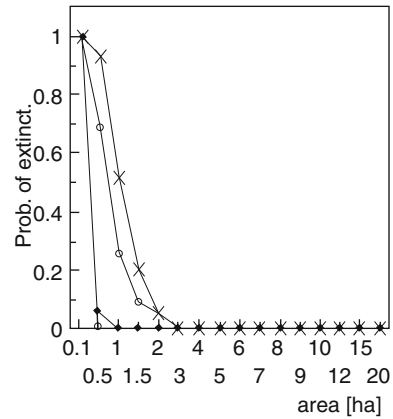
This result is used in Fig. 2.13 to determine the time to extinction. We find (note that the y-axis has a logarithmic scale) two intervals where the time to extinction is exponentially growing with R_0 . One is $R_0 \ll 1$, the other is $R_0 \gg 1$. The growth rate is for $R_0 \gg 1$ much higher than for $R_0 \ll 1$. Around $R_0 \approx 1$, we find an interface, connecting the two different slopes. We also find that for $R_0 < 1$ the time to extinction merely varies with population size N , while for $R_0 > 1$ the population size has an important influence. This is the case, as for $R_0 < 1$ only minor outbreaks take place. The size of minor outbreaks is more or less independent of N , in the sense that even for $N \rightarrow \infty$ the size of a minor outbreak is bounded. This is different in case of major outbreaks: the linear birth-death process will grow exponentially. Therefore, the logistic process will eventually reach a size about $N(1 - 1/R_0) = O(N)$. The larger N , the larger the equilibrium size, and the less likely touches the process $X_t = 0$ by chance. In the deterministic limes $N \rightarrow \infty$, we know that the time to extinction tends to infinity for $R_0 > 1$.

Application to Ecological Systems

The considerations above concerning the time to extinction and to separate the cases β/μ larger or smaller one (if N is finite) are not of merely academic interest. At least in principle, these considerations can be used e.g. to get an idea how large to choose a nature reserve for a certain species. The aim would be to choose this reserve in such a way that the species survives with a high probability a given time, e.g. 50 years. Unfortunately, a high effort is needed to set up a realistic model and to estimate the parameters of this model such that quantitative predictions are possible.

One case, where in fact this has been done is the investigation about a planned reservoir for a certain butterfly (*Maculinea arion* [96, 197]). This butterfly has a funny life cycle: the eggs are placed in thyme. The larvae hedge and have to hibernate. They do this in a tricky way: The larvae “tell” a certain species of ants (*myrmica sabuleti*) that they are larvae of these ants. Consequently, the ants move the butterfly-larvae into their nests. There, the larvae hibernate (the butterflies hatch in the nests of the ants in the next spring, and then have to hurry out before the ants become aware that tasty butterflies are in their nests). The complete model takes into consideration the density of butterfly, thyme plants and ant nests etc., and – in this way – is able to predict the survival of the butterfly population. One result (dependence of the area size) is shown in Fig. 2.14. We find, that at least an area with a size of 4 ha is desirable.

Fig. 2.14 Probability of extinction (after 50 years) for the butterfly population over the protected area. Different ant nest-densities are assumed (cross: 150, circle: 200, closed diamond: 250, open diamond: 300 nests per ha) (From: E.M. Griebeler et al. Verh. Ges. Ökol. 29 (1995), p.201–206, Fig. 4 [96] (with friendly permission of the author))



2.1.3 Further Limited Growth Models

Here, we consider some further possibilities to describe the limited growth of populations, exemplarily in the deterministic continuous case. They are more specialised to the behaviour of certain populations and their growth behaviour; also take into account further influences from the environment.

2.1.3.1 Sigmoid Growth

The first examples, following [220], belong to the class of so-called “S-shaped growth” models, also called “sigmoid growth”. The term “sigmoid” is not related to the shape of the model equations, but to the graph of the population size x over time t . One approach is the Gompertz equation,

$$\frac{dx}{dt} = r_0 e^{-\alpha t} x,$$

where the intrinsic rate of growth is assumed to decay exponentially in time. In the ecological context, this model is e.g. used for the growth of plants, or for some fishery ecology problems.

Remark The Gompertz equation, formulated in that way, is a non-autonomous ODE, i.e., there is a parameter which depends explicitly on time t . So, some typical tools for the analysis cannot be used since they are only valid or useful for autonomous ODEs.

Of course, there are many other approaches for a limited population growth, which are used for special cases – not all can be considered here in detail, e.g.

- Beverton-Holt:

$$\dot{x} = x \frac{1-x}{1+\alpha x}, \quad \text{where } \alpha \geq 0$$

- Ricker:

$$\dot{x} = x \frac{e^{\gamma(1-x)} - 1}{e^{\gamma} - 1}, \quad \text{where } \gamma \geq 0$$

Usually, these S-shaped growth models have two stationary points ($x = 0$ and a further $\bar{x} > 0$); they show a convex increase first, and later a concave decrease. For most of these models, there exist uniquely determined numbers

$$K > L > 0 \quad \text{such that } f(K) = 0 \text{ and } f'(L) = 0;$$

furthermore $x(t) \rightarrow K$ for $t \rightarrow \infty$. K is already known as carrying capacity, L is called the “population size with maximum growth”. Only few assumptions for F are necessary to lead to such a behaviour; for further details hereto see [220].

The typical ratio of K in L in our model examples are

- Continuous logistic growth (Verhulst): $K/L = 2$
- Beverton-Holt: $K/L > 2$
- Gompertz: $K/L = e$

This ratio may be useful for the model choice in a concrete case, e.g. if L is not around $K/2$ (in the observed data), then the logistic growth might be not an appropriate model approach.

2.1.3.2 Allee Effect

Two papers of Allee [2] gave the name to the Allee effect. The basic idea is to refine modelling the population growth in case of small population levels. Up to now, the basic assumption was that an increasing population density has a negative effect on reproduction/survival of a single individual. But for some cases it is sensible that an increase of the population density is beneficial and increases the stability of the population. Models, which take that into account, are called “Allee type models”.

Where does this effect come from? There are two main possibilities (see also [220]): It may be necessary to find a mate for reproduction, but the meeting probability may be low in case of small populations; and: It may be necessary to defend the group against a (so-called “generalist”) predator. Larger groups may have more power to defend themselves than small groups or even single individuals.

The model structure is based on a sigmoid growth model, supplemented by a term describing the extra mortality, which decreases with increasing population density. One very simple possibility is based on the Verhulst model, with an additional linear factor:

$$\dot{x} = rx \left(1 - \frac{x}{K}\right) \left(\frac{x}{K_0} - 1\right) =: f(x).$$

Obviously, there exist three stationary points: $\bar{x} = 0$, $\bar{x} = K_0$ and $\bar{x} = K$. The parameter K_0 corresponds to a minimal population size; if the population size happens to be below K_0 it will be driven to die out, subject to the effects mentioned above. So, the condition $0 < K_0 < K$ yields a reasonable modelling approach for the desired effect. In this case, $\bar{x} = 0$ is a stable stationary point, whereas $\bar{x} = K_0$ is unstable and $\bar{x} = K$ is again stable (see also Fig. 2.15). This means, we have a bistable situation (two stationary points are locally stable).

We mention here shortly the dependency of position and stability of the stationary points on the parameter K_0 . As we consider this parameter as the one governing the behaviour of the system, this parameter is also called “bifurcation parameter”. A “transcritical bifurcation” can be found at $K_0 = K$, i.e., two stationary points meet and exchange thereby their stability, see Fig. 2.16 for the so-called bifurcation diagram – the stationary points and their stability are drawn over the parameter K_0 . We will consider later the phenomenon of bifurcations in greater detail (Sect. 2.3.2.4). Of course, there are different approaches how to find suitable models for the Allee effect. E.g., Thieme [220] introduces a model for a female population size (under the assumption of a sex ratio in the population of about 1:1), which is split into two subpopulations: with and without a mate.

Fig. 2.15 Graph of the right-hand side function of the Allee model; the arrows on the x -axis indicate if the population grows or decreases

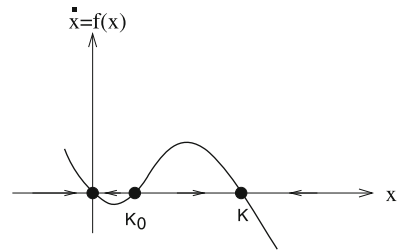
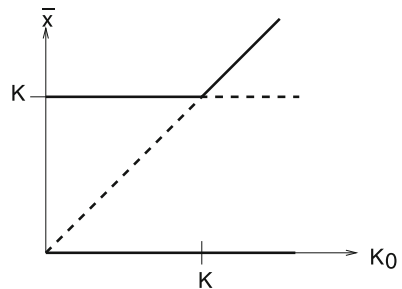


Fig. 2.16 Bifurcation diagram for the Allee model, K_0 is chosen as bifurcation parameter. The dotted line shows the unstable branch, the solid line the stable branch



2.1.4 Harvesting Problems

In this subsection we deal with the situation of a population (underlying again a sigmoid growth), which is additionally harvested. In this context, we do not consider the situation of a predator population which solely depends on the harvested population, but have in mind for example the situation of fishery: people like to eat fishes, but have also further food. The goal is to examine the consequences of harvesting on the harvested population.

As basis for the sigmoid growth, we choose the logistic equation – mainly for reasons of simplicity. Of course, also other approaches can be chosen, dependent on the behaviour of the population. We follow the approach introduced by [152] and consider a basic mode for a fish population, which is harvested. Apart of the parameters in the logistic model, a further variable is introduced: E , the so-called fishing effort. This effort is assumed to be constant. The fish captured per unit effort is assumed to be proportional to the available amount of fish, x :

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) - qEx$$

The proportionality constant q , the so-called “catchability”, describes how “easy” the fishes can be harvested. Then, qE corresponds to the “fishing mortality”, caused by the harvesting. (Remark: it has the same dimension as the growth parameter r .)

First, we compute the equilibria \bar{x} :

$$r\bar{x} \left(1 - \frac{\bar{x}}{K}\right) = qE\bar{x}.$$

Obviously, there are two equilibria:

$$\bar{x} = K \left(1 - \frac{qE}{r}\right) \quad \text{and} \quad \bar{x} = 0.$$

Figure 2.17 helps to understand about the stability behaviour. If the fishing mortality is quite small, then harvesting reduces the population level, below the carrying capacity K , but still allows survival of the population. The nontrivial stationary point \bar{x} is stable (which can be computed by considering the derivative, or just seen here in the figure). Vice versa, $\bar{x} = 0$ is unstable. If the fishing mortality is increased, then the straight line qEx becomes steeper. The position of the nontrivial \bar{x} moves to the left, but still stays positive and stable, if qE is not too large (i.e., if there is still the positive intersection point with the parabola). This works in that way, as long as $qE < r$. In the limit case $qE = r$, they only intersect in $\bar{x} = 0$. If we increase qE further, still $\bar{x} = 0$ is the only solution: This situation corresponds to a severe overfishing!

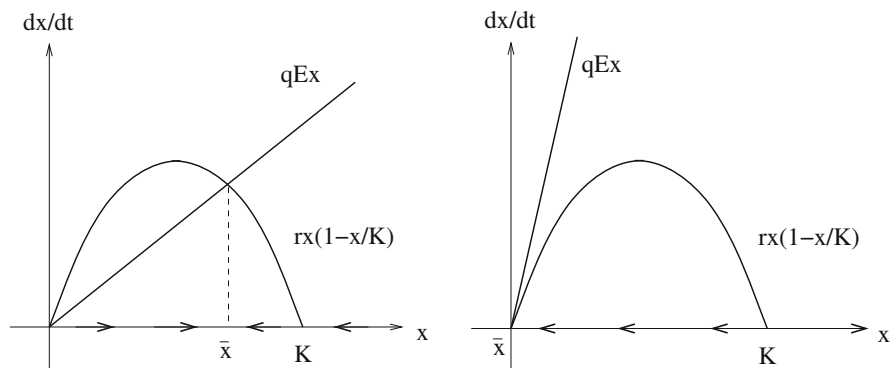


Fig. 2.17 Terms of the simple harvest model, showing the stationary points and their stability. *Left figure: small fishing mortality, right figure: severe overfishing*

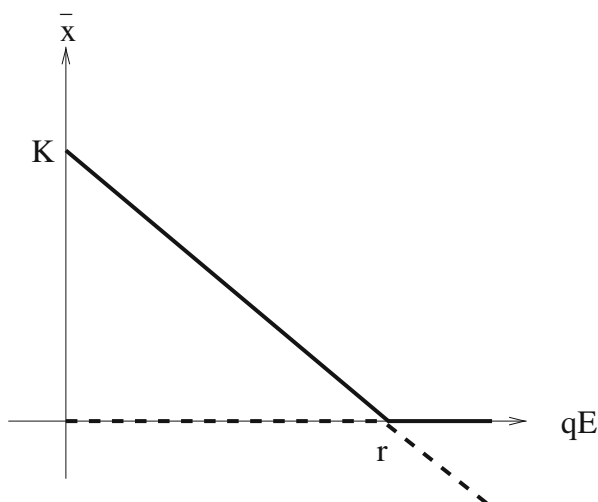


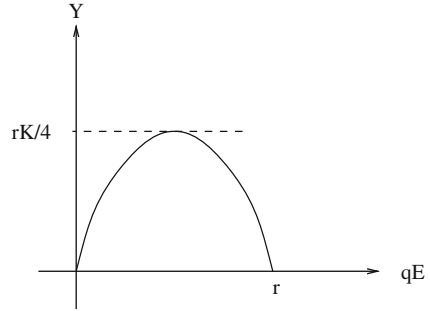
Fig. 2.18 Bifurcation diagram, using qE as bifurcation parameter. The *solid line* shows the stable branch, the *dashed line* the unstable branch

Obviously, the behaviour depends on the size of qE . In a similar way as in the preceding section, we can plot the corresponding bifurcation diagram (Fig. 2.18): Obviously, a transcritical bifurcation happens at $qE = r$, i.e., the two branches intersect each other and exchange their stability. From the ecological point of view, the graph shows the dependency of the equilibrium level of the fish population on the fishing mortality.

In the next step, we determine how much is harvested in the equilibrium situation (also called “sustainable yield”):

$$Y = qE\bar{x} = qEK \left(1 - \frac{qE}{r}\right).$$

Fig. 2.19 The Yield-effort curve for the basic harvest model



Plotting this function over qE (a parabola) yields the so-called “Yield-effort curve”, see Fig. 2.19. From that, we can see: If the fishing effort is increased, the sustainable yields increases, too, but only up to a certain point. Further increasing diminishes the sustainable yield again, for the harvested population it means: it is overexploited and depleted. Of course, we can also compute the optimal level of effort. The maximum sustainable yield (often denoted shortly by “MSY”) satisfies the condition

$$\frac{dY}{dE} = qK \left(1 - \frac{2qE}{r} \right) = 0,$$

which leads to

$$E_{MSY} = \frac{r}{2q} \quad \text{and} \quad MSY = \frac{rK}{4}$$

Up to now, our harvesting model was based on the assumption of logistic growth of the non-harvested population. Of course, further processes like the Allee effect for immigration/emigration may play a role.

Can we change the model (as we e.g. did before with the logistic equation in adding the Allee effect), and have a “robust” result? This is, does the system looks alike if we make small (whatever small does mean) changes? Or, to be more precise, what happens to the bifurcations, if small perturbations are introduced to the underlying ODE system? The ODE can be formulated as

$$\frac{dx}{dt} = f(x, \mu)$$

(μ is taken as the bifurcation or control parameter). For the analysis of the structural stability, the ODE is perturbed, i.e.

$$\frac{dx}{dt} = f(x, \mu) + \varepsilon g(x).$$

$g(x)$ can be chosen (arbitrary function); ε is the (small) amplitude of the structural perturbation. In general, $g(x)$ (which is also called sometimes “imperfection”) can be expanded in a Taylor series about the bifurcation point. Then, one can decide for the order, and thus only keep the lower-order terms.

Simple example: We take the well-known harvesting model and add a small constant I to it:

$$\frac{dx}{dt} = rx \left(1 - \frac{x}{K}\right) + I - qEx$$

Ecological meaning for the “imperfection”:

- $I > 0$: there is a constant immigration to the present population
- $I < 0$: there is a constant emigration to the present population

Exemplary bifurcation diagrams for small negative I , $I = 0$, and small positive I can be found in Fig. 2.20. There we see:

- Case of emigration: Instead of the transcritical bifurcation, there are two saddle-node bifurcations. There are regions, where no (real-valued) stationary point is present \leadsto catastrophic collapse of the fishery! (Positivity of solution is not conserved!)
- Case of immigration: There is no bifurcation at all!

Obviously, the qualitative behaviour of the bifurcation changes very much, dependent on the parameter I . This is the reason, why the transcritical bifurcation is considered to be “structurally unstable”. A nice theory about “unfolding” a bifurcation (as we did here with the transcritical bifurcation) can be found in the book of Golubitsky and Schaeffer [88].

There are further possibilities to refine the modelling approach. Taking harvesting as economic factor, one wants to find optimal harvesting strategies, the harvesting effort can be adapted to the present population. The harvesting effort can be introduced as a second dynamic equation; or the goal is to maximise the profit and by that introduce conditions for the harvesting effort. The latter leads to an optimal control problem. For more details, see e.g. [152].

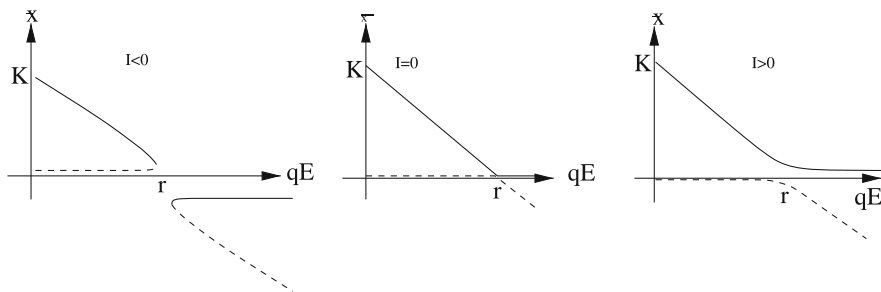


Fig. 2.20 Bifurcation diagram for the harvesting model, with emigration ($I < 0$) respectively immigration ($I > 0$). Solid lines show the stable branches, dashed lines the unstable branches

2.1.5 Conclusion

In this section, we have learnt how to formulate population models for one homogeneous species, where interactions in form of intra-species competition play a central role. First of all we understand that nonlinearity in deterministic models corresponds to dependencies in stochastic models. We have some idea how to use the limit of large population size to scale a deterministic model out of a stochastic model. The prototypical model is the logistic system. We investigated this model in different structures: deterministic and time-discrete, deterministic and time-continuous, and stochastic and time-continuous.

Let us start to summarise the most simple situation, the time-continuous and deterministic model. We have seen that the main tool to analyse non-linear models is the investigation of stationary points and their stability. The linear stability (the stability of the stationary point by means of linearised equations) and the stability of the nonlinear equations agree, as long as the eigenvalues of the linear system are non-zero (later we will see that we better say: have non-zero real part).

If the real part becomes zero, we find in general bifurcations (a qualitative change in the behaviour of the solutions). The typical bifurcation is the transcritical bifurcation for at a reproduction number $R_0 = 1$: for $R_0 < 1$, the population dies out, for $R_0 > 1$ it will settle on a stationary point which corresponds to a persistence of the population. The interactions (intra-species competition) prevents the population to increase its size for ever.

In the time-discrete case, we still can use the linear stability analysis, only the criterion that the eigenvalue has non-zero real part has to be replaced by the criterion that the absolute value of the eigenvalue must be different from 1. The behaviour of the time-discrete logistic equation is much more complex than the time-continuous logistic equation. We found that secondary bifurcations happen, i.e., the stationary point with a persisting population loses the stability (via period doubling bifurcations), and the population may even become chaotic via the period doubling route to chaos. This noise is hard to distinguish from intrinsic or extrinsic stochastic influences (small population size resp. external influences like weather).

The stochastic model exhibits similar features like the deterministic model. However, more advanced techniques are necessary to find these effects back, as they tend to be blurred by the intrinsic noise. In some sense, we always required that the population size becomes large in order to obtain some indication of the consequences of the dichotomy $R_0 < 1$ resp. $R_0 > 1$.

The transcritical bifurcation can be revealed via stochastic coupling of the logistic process and a linear birth-death process; if the population size is large, both processes agree for a long time. We know the probability for extinction of the linear process, hence, also the logistic process will have (also for $R_0 > 1$) only a certain probability to take off.

Next we seek for a criterion how to identify some solution that corresponds to the persisting solution in the deterministic model. The problem is that we know that the solution of the logistic process dies out almost sure. The way out is

the quasi-stationary solution, that indeed has a maximum at the location of the deterministic persisting solution in case of $R_0 > 1$, and is located at a zero population size if $R_0 < 1$. As a last important property we identified the different behaviour of the time to extinction in the two cases: while this time is short if $R_0 < 1$, it becomes large (especially for a large population size) if $R_0 > 1$.

All in all we found three properties that show that stochastic model and deterministic model express the same phenomena. We will use the mathematical techniques as well as the fundamental understanding of the effects over and over again in this and other chapters.

2.1.6 Exercises

Exercise 2.1 Consider the model of Varley, Gradwell and Hassell,

$$x_{t+1} = \frac{\lambda}{\alpha} x_t^{1-b}$$

which describes the limited growth of a population. λ denotes the average number of offspring, $1/\alpha x_t^{-b}$ the fraction of the population which survives up to reproductive adulthood. Determine the stationary state of this model, check the stability of these steady states, and interpret your results.

Exercise 2.2 Consider the time-discrete version of the Beverton-Holt model [25] introduced above for the time-continuous case,

$$x_{n+1} = \frac{r}{1 + x_n (r - 1)/K} x_n.$$

- (a) Interpret the model.
- (b) Use the transformation $y_n = 1/x_n$ and find an explicit representation $x_n = f(n)$ of a trajectory.

Exercise 2.3 We found that the wasp population discussed above is well described by a Ricker model with parameters $r = 5.4$ and $K = 5.7$. Do you expect the population to tend into a steady state?

Exercise 2.4 Consider the time-continuous stochastic logistic process,

$$\begin{aligned} P(X_{t+\Delta t} = X_t + 1) &= \beta X_t (1 - X_t/N) \Delta t + o(\Delta t), \\ P(X_{t+\Delta t} = X_t - 1) &= \mu X_t \Delta t + o(\Delta t). \end{aligned}$$

Show that the population eventually goes extinct with probability one:

(a) Prove that there is $\varepsilon > 0$ s.t.

$$P(X_{t+\Delta t} = 0 | X_t = k) \geq \varepsilon$$

for $k \leq N$.

(b) Define $p_n = P(X_{n\Delta t} = 0)$. Find a recursive equation for a lower bound of p_n using part (a).

(c) Show that $\lim_{n \rightarrow \infty} p_n = 1$.

Exercise 2.5 A fish population is growing according to the following law:

$$\dot{x} = \alpha x \ln \left(\frac{K}{x} \right) - qEx.$$

What does this equation mean biologically? Determine the equilibria, the yield curve and the maximum sustainable yield for the population.

Exercise 2.6 Another fish population is growing according to the following law:

$$\dot{x} = rx \left(\frac{x}{K_0} - 1 \right) \left(1 - \frac{x}{K} \right) - qEx.$$

(a) What does the threshold K_0 represent?

(b) Investigate the equilibria of the model.

(c) Plot the equilibria curve with respect to the fishing mortality (qE). What does that mean?

2.2 Metapopulation Models

Most populations do not just live in one single habitat, but are spread over several habitats. Even though such “small populations” may go extinct locally, the total population survives in many cases since individuals from neighbouring surviving habitats can invade and thus reoccupy it again. This type of problems is considered in the metapopulation theory. Typical questions are if a certain patchwork of local habitats is able to support a population for a long time, or which factors play a role for the survival.

Metapopulation models mainly start with the following idea: If a habitat is occupied, then the probability for extinction per time interval is relatively small. If the population breaks down, however, it happens (approximately) at one moment in time. Vice versa, if a population invades a patch, its local density will reach very soon the carrying capacity by logistic growth. Whereas the relative number of occupied spots changes relatively slowly. We find two clearly separated time

scales: the (fast) time scale of a local population, and the (slow) time scale of the relative number of occupied sites. Since we are primarily interested in the latter, we are allowed to always assume that local population are in an equilibrium – either (locally) extinct, or at the (local) carrying capacity.

2.2.1 *Levin's Basic Model*

The first metapopulation model was introduced by Levin in 1969. For that, $p(t)$ denotes the probability that a patch is occupied, and e is the rate by which a patches crash. Neglecting re-occupation for the moment, we obtain

$$\dot{p} = -ep.$$

Of course, re-occupation happens and is important. For the re-occupation, we need an empty patch (the probability of that is $1 - p$) and an individual which arrives from another patch. Since the number of individuals that may arrive is proportional to p , also the arrival rate is proportional to p . Taken together, the re-occupation rate is $cp(1 - p)$ and the resulting equation reads

$$\dot{p} = -ep + cp(1 - p).$$

Obviously, this is a logistic equation, which shows the typical threshold behaviour. For the persistence of the metapopulation, it is sufficient and necessary to have

$$e < c.$$

This model is the basis for all metapopulation models. Our main assumptions are: Homogeneous patches are considered (same size, isolation, habitat quality etc. for each population site). No spatial structure is taken into account; the “neighbourhood” is neglected, which means that the exchange between different population sites is always the same. There are no time lags, instantaneous changes are assumed. c and e are taken to be constant, independent of time. Demographic stochasticity can be neglected as we deal with a large number of patches.

Other models take this idea for refined approaches and by that explore the effect of the considered mechanisms.

2.2.2 *Habitat Destruction*

Habitat destruction is for sure one of the most important practical problems. Let us extend Levin's model by habitat destruction and investigate how a metapopulation

model reacts on this effect. Each site can assume one of the following three states:

1. State “1”: suitable site, unoccupied
2. State “2”: suitable site, occupied
3. State “3”: unsuitable site

Mainly two processes play a role in the metapopulation model:

1. A suitable occupied site can crash. The rate for a local extinction is e .
2. A suitable, but empty site can be re-occupied. The rate of reoccupation is c .

We distinguish two scenarios: (1) dynamic destruction, i.e., each site may be destructed at a certain rate γ but becomes suitable again at rate θ and (2) static loss, i.e., a certain fraction h of sites is unsuitable – basically these site are removed from the system.

Basic model without loss:

$$\begin{aligned}\dot{p}_1 &= ep_2 - cp_1p_2 \\ \dot{p}_2 &= -ep_2 + cp_1p_2 \\ \dot{p}_3 &= 0.\end{aligned}$$

As $p_1 + p_2 + p_3 = 1$ we find Levin's model back if $p_3(0) = 0$.

Model with static loss:

Here, we have the same model equations, but choose $p_3(0) = h$. I.e., a fraction h is not habitable. We find at once that the non-trivial stationary state of this system is given by

$$p_2 = 1 - h - \frac{e}{c}.$$

Model for dynamics loss:

In this case, a patch may become unsuited at rate γ and may return in the suited (but empty) class at rate θ

$$\begin{aligned}\dot{p}_1 &= ep_2 - cp_1p_2 - \gamma p_1 + \theta p_3 \\ \dot{p}_2 &= -ep_2 + cp_1p_2 - \gamma p_2 \\ \dot{p}_3 &= \gamma(p_1 + p_2) - \theta p_3.\end{aligned}$$

For the equilibrium situation we obtain

$$p_3 = \frac{\gamma}{\gamma + \theta} =: h$$

and

$$p_2 = 1 - h - \frac{e + \gamma}{c}.$$

Dynamic loss is more detrimental than static loss; even if the same fraction h is unsuited for the population, the fraction of occupied sites is less in case of dynamic loss. This is because γ acts as an additional death rate for occupied patches.

2.2.3 Rescue and Allee Effect

Coming back to our toy models, we focus on the extinction and re-occupation process in greater detail.

Rescue Effect

Levin's model assumes a constant extinction rate. But if a reasonable fraction of patches is occupied, there may be a constant immigration rate from these occupied patches into the given patch (even if it is not empty yet). So, it might happen that these immigrants rescue this patch (before it goes extinct at all) and by that, the patch "survives". We take this effect into account by decreasing the extinction rate if p is high, i.e., e is replaced by $e/(1 + \sqrt{\zeta p})$

$$\dot{p} = c(1-p)p - e \frac{p}{1 + \sqrt{\zeta p}} = p \left[c(1-p) - e/(1 + \sqrt{\zeta p}) \right].$$

There is always one stationary state: $p = 0$. For the other stationary state, we find the condition

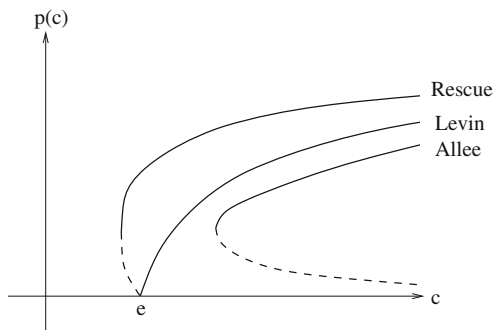
$$c = c(p) = \frac{e}{(1 + \sqrt{\zeta p})(1 - p)}.$$

We can see: $c(0) = e$, that means that the nontrivial line of stationary points hits the line $p = 0$ at the same position as Levin's model does. For a sketch of the graph see Fig. 2.21 (including also the Allee effect).

Allee Effect

Considering sexually reproducing species, it is clear, that at least two (and mostly even considerably more) individuals are required for survival of the population. It does not help much if just one individual enters an empty patch: at least two individuals (a male and a female) are needed to start a new population. We meet again the Allee effect! If the probability that one individual enters the patch under consideration in a given time interval is proportional to p , then the probability that

Fig. 2.21 Comparison of the stationary solutions of Levin's, Allee and rescue model. The *dashed lines* indicate unstable, nontrivial stationary points, the *solid lines* stable ones (Remark that the trivial one $p = 0$ is left out in the figure)



two individuals enter it in the given time interval is proportional to p^2 . Hence, the modified model reads

$$\dot{p} = c(1-p)p^2 - ep.$$

In the same way as for the rescue effect, the lines of stationary points can be determined: the trivial line ($p = 0$) and the nontrivial line $c(p) = e/p(1-p)$. In the case of the Allee effect, the nontrivial line never intersects the trivial line; all points above a critical value for c are bistable. The curve is sketched in Fig. 2.21. Obviously both, the rescue effect and the Allee effect lead to a bistable parameter region. The immigration parameter c , which we use as a bifurcation parameter, corresponds to the habitat density. Only Levin's basic model shows a continuous dependency of the population size on c . Due to the "blue sky bifurcation" and its bistable behaviour, the rescue- as well as the Allee effect model may sustain the population size at a relatively high level, until they crash down suddenly when c becomes too small. From a biological point of view, this can be interpreted as follows: Also a relatively high (meta)population level does not necessarily reflect a "safe situation", where no risk for (global) extinction of the metapopulation is present. Such a behaviour can also be found in some experimental data. E.g. Hanski et al. [109] investigated a large patchwork of habitats for a species of butterflies *Militaea cinxia* in the south-west of Finland. Thousand five hundred and thirty habitats were located (small spots of 12 m^2 up to large habitats with 7.3 ha). These habitats were distributed over an area of $3,500 \text{ km}^2$. In each of the habitats, the population size was measured in 1993 and 1994. These data showed the Allee effect. Even bistability has been visible in the data.

2.2.4 Heterogeneity in Patch Size

The Levine model assumed that all patches have approximately the same size. Of course, this is not realistic; a different, extreme case is that there is one very big patch

(called the mainland) and a lot of small patches (islands), basically coupling to the mainland. The mainland can never die out. The islands die at a rate e , but become re-occupied at rate c . Reoccupation does not depend on p as this reoccupation is due to the mainland population. Thus, the fraction of occupied islands reads

$$\dot{p} = -ep + c(1 - p).$$

This is, we have two extreme cases

$$\begin{array}{ll} \text{Levin} & \dot{p} = cp(1 - p) - ep \\ \text{Mainland-Island} & \dot{p} = c(1 - p) - ep \end{array}$$

It is desirable to allow for a size distribution and not to focus on extreme cases. The Hanski model takes this approach. There is a nice derivation of this model using a size-structured approach [108]. Here, we give a rather heuristic explanation. We introduce an additional parameter a that reflects the size distribution of the patches; $a = 0$, indicates that all patches have equal size (Levin's model), while the limit $a \rightarrow \infty$ stands for the mainland-island model. a close to one does mean that there are some large patches and many small patches. We think about re-occupation and extinction for different patch-size distributions.

Re-Occupation:

We aim at a function that basically interpolates between $cp(1 - p)$ and $c(1 - p)$; choose

$$c(1 - p) \frac{(1 + a)p}{1 + ap}.$$

Extinction:

This term is more subtle. If $a = 0$ or $a \rightarrow \infty$ we assume that the rate of extinction is e . For $0 < a < \infty$ we assume to have some large patches that are more stable than the average. Thus, in-between the Levin and the mainland/island model, the extinction rate should be smaller. We define

$$e \left[\frac{a}{1 + a} + \frac{p}{a + p} \right] p.$$

All in all, the Hanski model reads

$$\dot{p} = c(1 - p) \frac{(1 + a)p}{1 + ap} - e \left[\frac{a}{1 + a} + \frac{p}{a + p} \right] p.$$

This model is more appropriate for practical purposes, though we still do not incorporate space explicitly.

2.2.5 Conclusion

Metapopulation models are based on the observation, that most individuals do not live homogeneously mixed, but are clustered in some way. This structure allows for local extinction and re-occupation. In general, the dynamics becomes highly complex. The central idea of Levin has been a decoupling of time scales: the process of going extinct resp. re-occupation is fast in comparison with the time scale at which the fraction of occupied patches changes. This idea allows to focus on the fraction of occupied patches, which yields relatively simple differential equations. Allee- and rescue effects are rather unexpected, but yield reasonable results that can be found back in field data.

2.2.6 Exercises

Exercise 2.7 Feng and De Woody [239] developed a new concept of metapopulation models that combines features of a spatial model with dynamic changes and patch quality. Defining $p_2(t)$ as the probability that a patch is habitable and occupied, the model reads

$$\frac{dp_2(t)}{dt} = c(\rho)(1 - p_2(t)) - e(\rho)p_2(t),$$

where ρ is the occupation probability of the patch, $c(\rho)$ is the colonisation rate of the patch when it is empty and $e(\rho)$ is the extinction rate of the patch when it is occupied.

Moving on from the idea of Feng and De Woody, give a mathematical model in which the patch is described by the following probabilities:

$p_0(t)$: = probability that the patch is inhabitable at time t

$p_1(t)$: = probability that the patch is habitable but empty at time t

$p_2(t)$: = probability that the patch is habitable and occupied at time t .

This metapopulation model is now defined by a three dimensional system. Which kind of assumptions could be made, in order to reduce it to a two dimensional system? Why would it be more comfortable to work with a two dimensional system?

2.3 Interacting Populations

Until now, we focused on one single species, neglecting possible direct or indirect interactions with other species. Of course, in reality more species are interdependent in different ways, ending up with complete food chain and food web systems. These large systems are difficult to understand by means of mathematical and

theoretical tools. We therefore start off with simple motives (simple and small toy systems exhibiting typical structures that can be found in real-world systems) and analyse these motives. The relationship between two populations can be various: the most famous example are for sure predator-prey systems. Therefore also we start with this structure. Parasite-host systems are in principle similar to predator-prey systems; the difference can be seen in the importance of generations for parasites, leading to time-discrete generation-driven models. In a second type of models, the populations do not interact directly, but compete for resources. A nice setting, where this competition is explicitly addressed is the chemostat. This is a device used in experiments, also called Continuously Stirred Tank Reactor (CSTR): there is a continuous inflow of liquid, and (in order to keep the volume constant), also an outflow. With the inflow, nutrients come in, the outflow removes nutrients, metabolic products, and microorganisms. As this device is frequently used, we will investigate models for chemostats in depth. More general models for competition, the Volterra model, that are not explicit in the mechanism of competition (in not addressing the resource the individuals compete for) are addressed afterwards; Mutualism or symbiosis models will only briefly touched.

However, before we investigate models we first introduce some mathematical tools for the analysis of nonlinear systems of ODEs.

2.3.1 Basic Tools for Nonlinear Systems

In this section, we introduce three tools frequently used in the long term analysis of an ODE: (a) Stability analysis of stationary points, (b) exclusion of complex behaviour like periodic orbits or even chaotic behaviour, and (c) reduction of the complexity by means of removing explicit time dependence if this dependence vanishes fast enough.

(a) *Stability analysis of stationary points.* A simple idea for the analysis of nonlinear systems is to use a linearisation, as already mentioned for the one-dimensional ODE case. Let us start with a two-dimensional system that has a stationary point at (\bar{x}, \bar{y}) . A perturbation is assumed

$$x = \bar{x} + u, \quad y = \bar{y} + v,$$

this yields

$$\begin{aligned} \dot{x} = (\bar{x} + u)' &= f(\bar{x} + u, \bar{y} + v) = \underbrace{f(\bar{x}, \bar{y})}_{=0} + \frac{\partial f(\bar{x}, \bar{y})}{\partial x} u + \frac{\partial f(\bar{x}, \bar{y})}{\partial y} v + \dots \\ \dot{y} = (\bar{y} + v)' &= g(\bar{x} + u, \bar{y} + v) = \underbrace{g(\bar{x}, \bar{y})}_{=0} + \frac{\partial g(\bar{x}, \bar{y})}{\partial x} u + \frac{\partial g(\bar{x}, \bar{y})}{\partial y} v + \dots \end{aligned}$$

Close to the stationary point, we neglect higher order terms and find approximately

$$\begin{aligned}\dot{u} &= \frac{\partial f}{\partial x}u + \frac{\partial f}{\partial y}v \\ \dot{v} &= \frac{\partial g}{\partial x}u + \frac{\partial g}{\partial y}v\end{aligned}$$

More generally, in dimension n , we consider a vector field $f : \mathbb{R}^n \rightarrow \mathbb{R}^n$ (to each point in \mathbb{R}^n a velocity vector in \mathbb{R}^n is assigned), and

$$\dot{x} = f(x), \quad f \in C^1(\mathbb{R}^n, \mathbb{R}^n), \quad f(\bar{x}) = 0, \quad \bar{x} \in \mathbb{R}^n,$$

Solutions $x(t)$ of that equation in the neighbourhood of \bar{x} are represented by a local coordinate system with origin \bar{x} , i.e., by $x(t) = \bar{x} + y(t)$. Then,

$$\dot{y}(t) = f'(\bar{x})y(t) + o(\|y\|).$$

The corresponding linearised system reads

$$\dot{z} = Az, \quad \text{where } A = f'(\bar{x}) = \left(\frac{\partial f_i}{\partial x_k}(\bar{x}) \right).$$

The stability behaviour of a stationary state can often be determined easily from the eigenvalues of the Jacobian matrix.

Proposition 2.17 (Linearisation, Stability, Perron, Lyapunov) *If the real parts of all eigenvalues of $A = f'(\bar{x})$ are negative, then \bar{x} is exponentially asymptotically stable, i.e., there are constants $\delta, C, \alpha > 0$, such that $\|x(0) - \bar{x}\| < \delta$ implies*

$$\|x(t) - \bar{x}\| < Ce^{-\alpha t} \quad \text{for } t \geq 0.$$

Addendum:

From $\operatorname{Re} \sigma(A) \cap (0, \infty) \neq \emptyset$ it follows that \bar{x} is unstable (for more details, see [3]).

As this is a quite rough (but also useful) statement, the following question appears: When do linear and nonlinear model “correspond” locally? The answer is given by the next proposition.

Definition 2.18 \bar{x} is called hyperbolic, if $0 \notin \operatorname{Re} \sigma(f'(\bar{x}))$.

Theorem 2.19 (Hartman [110] and Grobman [97]) *Let \bar{x} be hyperbolic. Then, there is a neighbourhood U of \bar{x} and a homeomorphism $H : U \rightarrow \mathbb{R}^n$ with $H(\bar{x}) = 0$, which maps the trajectories of $\dot{x} = f(x)$ one-to-one into trajectories of $\dot{z} = Az$, with respect to the time course.*

This is, if $x(t)$ is a solution of the nonlinear system, $z(t) = H(x(t))$ is a solution of the linear system (as long as $x(t)$ does not leave U). The converse is also true: if $z(t)$ is a solution of the linear system, $x(t) = H^{-1}(z(t))$ solves the nonlinear system (again, as long as $x(t)$ is contained in U). One may visualise the homeomorphism H as a rubber skin. Just by stretching the rubber skin, the nonlinear system can be (locally) transformed in a linear system.

We formulate the same statement in a less formal description for two dimensions: Let $\operatorname{Re} \lambda_j \neq 0$ for all j . Then all solution curves of the nonlinear system

$$\begin{aligned}\dot{x} &= f(x, y) \\ \dot{y} &= g(x, y)\end{aligned}$$

show the same qualitative behaviour at the stationary point (\bar{x}, \bar{y}) as those of the corresponding linear problem.

$$\begin{pmatrix} \dot{u} \\ \dot{v} \end{pmatrix} = \begin{pmatrix} \frac{\partial f}{\partial u} & \frac{\partial f}{\partial v} \\ \frac{\partial g}{\partial u} & \frac{\partial g}{\partial v} \end{pmatrix} \begin{pmatrix} u \\ v \end{pmatrix}$$

(derivatives at (\bar{x}, \bar{y})). The nice thing is, that we classified the behaviour of a linear two-dimensional system completely (Sect. 1.3.2). We can use our understanding of linear equations to understand nonlinear equations locally at a stationary point.

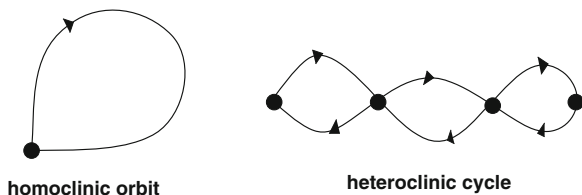
Remark We emphasise that this theorem is not valid for $\operatorname{Re} \lambda = 0$ (the so-called marginal stability of the linearised equation), i.e., there are e.g. problems with the examination of centres and spirals.

In order to obtain an impression of an ODE $x' = f(x)$, in particular in two dimensions, one often considers curves where the vector field is parallel to a coordinate axis. These curves are named isoclines. In two dimensions, $x' = f(x, y)$ and $y' = g(x, y)$, the x -isocline is the curve defined by $f(x, y) = 0$, while the y -isocline is given by $g(x, y) = 0$. Stationary points are located at the intersection of an x and y isocline.

(b) *Existence/Exclusion of periodic orbits.* After the positions and the stability of stationary points are determined, it might be interesting to know if the long term behaviour of a solution is a stationary point or another object, e.g. a periodic orbit. In order to be able to better talk about long term behaviour we introduce some definitions.

Definition 2.20 Consider a ODE $x' = f(x, t)$, $x \in \mathbb{R}^n$. A solution $x(t)$ with initial condition x_0 is called trajectory of x_0 . A non-constant trajectory with $x(t+T) = x(t)$ for some $T > 0$ is called a periodic orbit. A non-constant trajectory $x(t)$ that ends at a stationary point x_1 and starts at a stationary point x_2 (i.e., $\lim_{t \rightarrow -\infty} x(t) = x_2$, $\lim_{t \rightarrow \infty} x(t) = x_1$) is called heteroclinic orbit if $x_1 \neq x_2$ and homoclinic orbit else. A heteroclinic cycle is a finite number of heteroclinic orbits, connecting n stationary points in a cyclic manner; see also Fig. 2.22.

Fig. 2.22 Sketch of a homoclinic orbit (*left figure*) and a heteroclinic chain (*right figure*)



Having specified some candidates for long term behaviour, we define a general class of sets that indeed characterise the fate of a trajectory.

Definition 2.21 (ω — limit set) Consider a trajectory $x(t)$ with initial value x_0 . The ω limit set of x_0 is given by

$$\omega(x_0) = \{y \mid \exists(t_n), t_n \nearrow \infty, y = \lim_{n \rightarrow \infty} x(t_n)\}.$$

This definition allows apart of stationary points also periodic orbits and heteroclinic cycles to be an ω -limit set. Thereto only sequences of time points that tend to infinity are considered, not $\lim_{t \rightarrow \infty} x(t)$ itself.

In order to determine ω -limit sets, we introduce some tools [98, 119]. We briefly note that a region is called positively invariant, if a trajectory may enter but never leave this region.

Theorem 2.22 (Poincaré-Bendixson) Consider a trajectory $x(t) \in \mathbb{R}^2$ (or $x(t) \in D$, where $D \subset \mathbb{R}^2$ is compact and connected, positively invariant) of the ODE $\dot{x} = f(x)$, f smooth, with only finitely many roots. If $x(t)$ is bounded, then the ω -limit set is one of the following objects:

- A stationary point
- A periodic orbit
- A homoclinic orbit or heteroclinic cycle.

The direct consequence of this Theorem is: If there is no stationary point, there has to be a periodic orbit.

Remark 2.23 This proposition is not valid in higher dimensional spaces (or on a torus)! A famous counterexample is the Lorenz attractor, a chaotic ω -limit set of a three-dimensional ODE.

A typical situation where the Theorem of Poincaré-Bendixson can be applied in a very useful way, is shown in Fig. 2.23. In this case, the only remaining possibility is a periodic orbit, if further stationary points can be excluded. In some cases, the existence of loops (periodic orbits, homoclinic orbits, or heteroclinic cycles) can be excluded by the so-called negative criterion of Bendixson(-Dulac) [98].

Proposition 2.24 (Negative criterion of Bendixson) Let $D \subseteq \mathbb{R}^2$ be a simply connected region and $(f, g) \in C^1(D, \mathbb{R})$ with $\text{div}(f, g) = \frac{\partial f}{\partial x} + \frac{\partial g}{\partial y}$ being not

Fig. 2.23 Typical situation for the application of the theorem of Poincaré-Bendixon: An unstable stationary point (with solutions leaving it in all directions) inside a positive invariant area, no further stationary points present

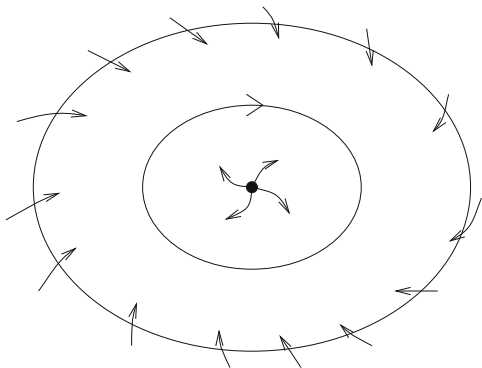
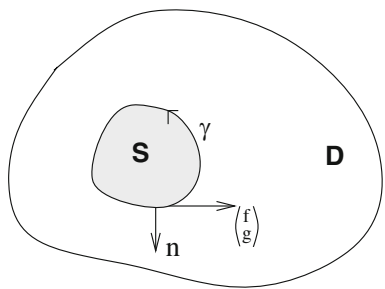


Fig. 2.24 Geometric situation for the proof of the negative criterion of Bendixson and Dulac



identically zero and without change of sign in D . Then the system

$$\dot{x} = f(x, y)$$

$$\dot{y} = g(x, y)$$

has no loop lying entirely in D .

Proof Consider a loop. This loop forms a smooth curve γ (with a discrete set of exceptions in case of homoclinic trajectories or heteroclinic cycles). As the curve is a trajectory, the vector field is tangential to the curve. Let $n(x, y)$ denote the outer normal vector to the region bounded by the loop. As the normal vector is perpendicular to the tangent vector, the scalar product between tangent vector and normal vector is always zero. The divergence theorem yields

$$0 = \int_{\gamma} \begin{pmatrix} f(x, y) \\ g(x, y) \end{pmatrix} n(x, y) d\tau = \int \int_S \left(\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} \right) dx dy = 0,$$

where S is the interior of γ , see Fig. 2.24. If $\frac{\partial f}{\partial x} + \frac{\partial g}{\partial y} > 0$ (or < 0) holds on D , then there is no region $S \subseteq D$ such that the integral over the divergence of the vector field (i.e., over $f_x + g_y$) becomes zero. Hence, it is not possible to have closed orbits which lie entirely in D . \square

The negative criterion of Bendixson can also be generalised; the same idea also works out for the system

$$\begin{aligned}\dot{x} &= \rho(x, y)f(x, y) \\ \dot{y} &= \rho(x, y)g(x, y),\end{aligned}$$

where $\rho > 0$ is continuously differentiable. In particular we are allowed to rescale a vector field by a scalar function (as long as this function has no zeros), before we show that the divergence is positive (or negative); we are allowed to check if the term

$$(\rho(x, y)f(x, y))_x + (\rho(x, y)g(x, y))_y$$

possesses a sign. This degree of freedom will be of importance in our applications.

Remark 2.25 Also the negative criterion can be applied only in the 2D case!

(c) *Asymptotic autonomous systems.* A last tool is the reduction of a non-autonomous system to an autonomous system in case that the non-autonomous aspect vanishes fast enough.

Theorem 2.26 *Let $x' = f(x, t)$ denote a non-autonomous system, and assume that there is a function $g(x)$ s.t. $|f(x, t) - g(x)|_{C^0} \leq Ce^{-\mu t}$ for $\mu > 0$. Assume that the ω -limits sets of $x' = g(x)$ consist of isolated stationary point, and no heteroclinic or homoclinic cycle is present. Then each bounded orbit of $x' = f(x, t)$ tends to one of these stationary points.*

The proof can be found in a paper by Thieme [219]. In general, the assumption (exponentially fast convergence) cannot be relaxed. One is tempted to conclude that the ω -limit sets of both systems always agree in some sense (and indeed, there are papers that wrongly work with such a strong conclusion), but it is possible to find counterexamples (see the paper of Thieme [219]).

2.3.2 Predator-Prey Models

2.3.2.1 Predator-Prey Model of Lotka-Volterra

We start with the historically first predator prey model, one of the most famous equations in mathematical biology.

The observation of d'Ancona (an Italian biologist), who studied the populations of various fish species in the Adriatic Sea was that the fraction of sharks at fishing in the Adriatic Sea varied from $\sim 11\%$ before the first world war to $\sim 30\%$ during the war, and back to $\sim 11\%$ after the war. What could the war have to do with the fishery? Is there a reasonable explanation for this fact? D'Ancona asked the famous

Italian mathematician Vito Volterra (1860–1940), his father-in-law, if he could put up a mathematical model to explain that observation (there wasn't any reasonable biological/ecological explanation available).

The modelling approach, introduced by Volterra [228] and Lotka [163] used two variables: Let x be the prey (eatable fishes), y the predators (Mediterranean sharks, skates, rays etc.). The ODE model reads [163]:

$$\dot{x} = ax - bxy \quad (2.6)$$

$$\dot{y} = -dy + cxy. \quad (2.7)$$

We start by computing the stationary points via the isoclines, see Fig. 2.25:

$$\dot{x} = ax - bxy = 0 \Leftrightarrow x = 0 \text{ or } y = \frac{a}{b} \quad \text{drawn in black}$$

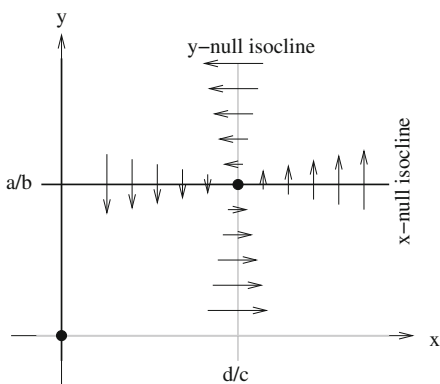
$$\dot{y} = cxy - dy = 0 \Leftrightarrow y = 0 \text{ or } x = \frac{d}{c} \quad \text{drawn in grey}$$

Hence, $(0, 0)$ and $(\frac{d}{c}, \frac{a}{b})$ are stationary points. $(\frac{d}{c}, \frac{a}{b})$ is called “coexistence point” or “nontrivial stationary point”. For the examination of the stability of the stationary points, we try to use the linearisation, i.e., the general Jacobian matrix is required:

$$\begin{pmatrix} \frac{\partial f}{\partial x} & \frac{\partial f}{\partial y} \\ \frac{\partial g}{\partial x} & \frac{\partial g}{\partial y} \end{pmatrix} = \begin{pmatrix} a - by & -bx \\ cy & cx - d \end{pmatrix}.$$

- In $(0, 0)$, the Jacobian matrix reads $\begin{pmatrix} a & 0 \\ 0 & -d \end{pmatrix}$
 \Rightarrow the eigenvalues are $a, -d$
 $\Rightarrow (0, 0)$ is a saddle point (thus unstable)

Fig. 2.25 Isoclines for the Lotka-Volterra predator prey model ($\dot{x} = 0$: black line, $\dot{y} = 0$: grey line)



- In $(\frac{d}{c}, \frac{a}{b})$, the Jacobian matrix reads: $\begin{pmatrix} a - b\frac{a}{b} & -b\frac{d}{c} \\ c\frac{a}{b} & c\frac{d}{c} - d \end{pmatrix} = \begin{pmatrix} 0 & -\frac{bd}{c} \\ \frac{ca}{b} & 0 \end{pmatrix}$
 $tr = 0, det = \frac{abcd}{bc} = ad$, thus:

$$\lambda_{1,2} = \frac{tr}{2} \pm \sqrt{\frac{tr^2}{4} - det} = \pm i\sqrt{ad} \quad (\text{purely imaginary}).$$

As the Theorem of Hartman-Grobman cannot be applied, no statement about stability possible at the moment $-(\frac{d}{c}, \frac{a}{b})$ could be a (stable or unstable) spiral or a centre (with closed solution curves around). We cannot decide that by linearisation! The nonlinear system, as it is, is structurally unstable. This means: Small perturbations of the vector field may lead to a complete change in the stability behaviour.

So, further tools are needed to examine stability of stationary points. We try the following approach: An invariant of motion $E(x, y)$ satisfies the equation

$$\frac{d}{dt}E(x(t), y(t)) = \frac{\partial E}{\partial x} \cdot \dot{x} + \frac{\partial E}{\partial y} \cdot \dot{y} = 0$$

The variable $E(x, y)$ does not change during time course, along a solution curve. Descriptive meaning: $E(x, y)$ is a kind of “mountains” over the x, y plane, $\frac{d}{dt}E(x(t), y(t)) = 0$ means that a trajectory lies on a level curve of E .

A physical interpretation would consider $E(x, y)$ to be an energy, a direct biological interpretation of $E(x, y)$ is more difficult, and such a function is also more difficult to find in general.

How to find such an invariant of motion? In the present case we are lucky. Separation of variables is possible and yields the desired result. Starting from the model equations, we obtain for $y \neq a/b$

$$\frac{dy}{dx} = \frac{y(cx - d)}{x(a - by)},$$

which describes the slope of the vector field in the phase plane (for the vector field, see Fig. 2.26). Using separation of variables yields

$$\begin{aligned} \frac{a - by}{y} dy &= \frac{cx - d}{x} dx \quad \Leftrightarrow \quad \left(\frac{a}{y} - b\right) dy = \left(c - \frac{d}{x}\right) dx \\ \Leftrightarrow \quad a \ln y - by &= cx - d \ln x + const. \end{aligned}$$

These findings suggest the following ansatz:

$$E(x, y) = d \ln x - cx + a \ln y - by,$$

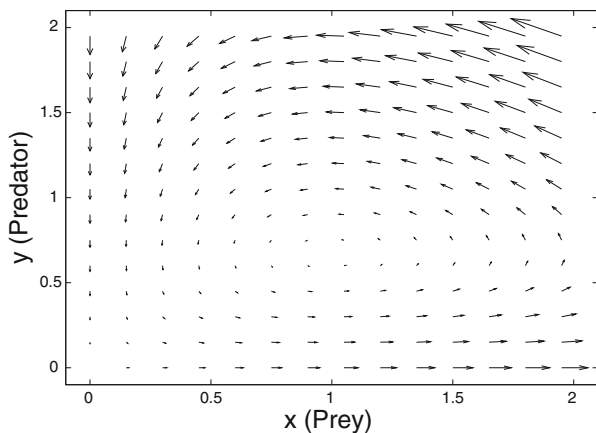


Fig. 2.26 Vector field of the Lotka Volterra predator prey model (2.6), (2.7); the arbitrarily chosen parameter values (dimensionless, just exemplarily), are $a = 1$, $b = 1.5$, $c = 1$, $d = 1$

which yields

$$\begin{aligned} \frac{d}{dt}E(x(t), y(t)) &= \left(\frac{d}{x} - c\right)(ax - bxy) + \left(\frac{a}{y} - b\right)(cxy - dy) \\ &= (d - cx)(a - by) + (a - by)(cx - d) \\ &= 0. \end{aligned}$$

Obviously, the chosen $E(x, y)$ is indeed an invariant of motion for the chosen predator prey model.

In order to determine the shape of the mountains, consider Fig. 2.27: The graph of $E(x, y)$ possesses one unique maximum at the coexistence point (work out the derivatives!). We find, that E resembles a mountain with one tip, with closed level curves and thus closed curves as solution trajectories.

Hence, the coexistence point of the Lotka-Volterra predator prey model is no spiral; the fish and the shark populations underlie oscillations. Nevertheless, the observations average in some sense over a long time interval. They show temporal means. Therefore we consider the temporal means resulting from the model equations.

Proposition 2.27 *Temporal means of solutions curves of the Lotka-Volterra model (2.6), (2.7) over one period are constant, independent from the initial point (but amplitude and periodic time are not!).*

Let T be the periodic time, thus $x(T) = x(0)$, $y(T) = y(0)$. Then:

$$\frac{1}{T} \int_0^T x(t) dt = \bar{x} = d/c. \text{ and } \frac{1}{T} \int_0^T y(t) dt = \bar{y} = a/b.$$

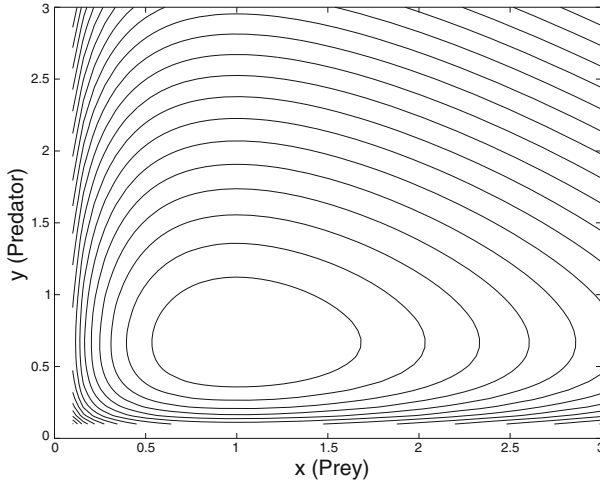


Fig. 2.27 Level set curves of $E(x, y)$, the invariant of motion for the Lotka-Volterra predator prey model; the arbitrarily chosen parameter values (dimensionless, just exemplarily), are $a = 1$, $b = 1.5$, $c = 1$, $d = 1$, same as in Fig. 2.26

Proof Generally, $\frac{d}{dt}(\ln(x)) = \frac{\dot{x}}{x} = a - by$, thus

$$\int_0^T \frac{d}{dt}(\ln(x(t))) dt = \int_0^T a - by(t) dt.$$

Then, it follows that

$$\begin{aligned} 0 &= \ln(x(T)) - \ln(x(0)) \\ &= aT - b \int_0^T y(t) dt \end{aligned}$$

and $\frac{1}{T} \int_0^T y(t) dt = \frac{a}{b} = \bar{y}$. The other equation can be shown analogously. \square

Conclusion: A non-recurring decimation of the predators does not have any influence on the mean values (there is just another trajectory chosen, with the same mean value).

We now include fishery at rate $\varepsilon > 0$, and derive at

$$\begin{aligned} \dot{x} &= ax - bxy - \varepsilon_1 x = (a - \varepsilon_1)x - bxy \\ \dot{y} &= cxy - dy - \varepsilon_2 y = -(d + \varepsilon_2)y + cxy \end{aligned}$$

(under the assumption that the crop of fishing is proportional to the fish population). Then the coordinates of the coexistence point are

$$\left(\frac{d + \varepsilon_2}{c}, \frac{a - \varepsilon_1}{b} \right),$$

which means: more fishing leads to more prey, less predators; vice versa, less fishing results in less prey, more predators. Here we find a phenomenon that is rather unexpected: the surplus of energy in the system (less harvesting) does not increase the prey abundance; the predator harvest the energy and grow until the prey is at the same levels (or even less) as before.

Coming back to the question of d'Ancona, the answer is that lacking fishery (due to the first world war) leads to a higher level of predators (in the mean). After starting more fishery again, the predators assume lower levels again.

2.3.2.2 Lyapunov Functions

Until now, we only proved local results concerning stability using linearisation and the theorem of Hartman-Grobman. These concepts only “work” in a small neighbourhood of a stationary point under consideration. But of course it would be very interesting to know something about the global (or at least “locally less limited”) behaviour of solutions. Furthermore, as we have already seen, linearisation does not always give an information about stability. So, additional tools are needed. In the case of the Lotka-Volterra model, the investigation of the “energy”-function $E(x, y)$ has been successful. We extend this idea, and end up with the so-called Lyapunov functions [98, 119, 147]. First we consider a Lyapunov function which is connected to a certain stationary point \bar{x} of an ODE. It is defined as follows (note that for $x \in \mathbb{R}^n$, the vector x^* is the transposed vector):

Definition 2.28 (Lyapunov function) Let $\bar{x} \in \mathbb{R}^n$ be a stationary point for the ODE

$$\dot{x} = f(x), \quad x \in \mathbb{R}^n, \quad f : U \rightarrow \mathbb{R}^n, \quad U \subseteq \mathbb{R}^n,$$

(i.e., $f(\bar{x}) = 0$). A function $V : W \rightarrow \mathbb{R}$ which is defined on some open neighbourhood $W \subseteq U$ of \bar{x} is called Lyapunov function of \bar{x} in W , if the following three conditions are satisfied:

- (a) $V \in C^1(W, \mathbb{R})$
- (b) $V(\bar{x}) = 0$ and $V(x) > 0$ if $x \in W \setminus \{\bar{x}\}$
- (c) $\dot{V}(x) = (\text{grad } V(x))^* f(x) = \sum_{j=1}^n \frac{\partial V}{\partial x_j} \dot{x}_j = \sum_{j=1}^n \frac{\partial V}{\partial x_j} f_j(x) \leq 0$ for $x \in W$.

If $\dot{V}(x) < 0$ for $x \neq \bar{x}$, then V is called a strong Lyapunov function of \bar{x} in W .

Remark 2.29 \dot{V} is the derivative of V along solution curves of the ODE.

How to use such a Lyapunov function?

The idea of an attracting stationary point can be generalised, a domain (or basin) of attraction can be defined as follows:

$$\mathcal{A}(\bar{x}) = \{x_0 \in \mathbb{R}^n \mid \lim_{t \rightarrow \infty} \|x(t) - \bar{x}\| = 0 \text{ with } x(0) = x_0\}.$$

Theorem 2.30 (Lyapunov, Smale) *If \bar{x} possesses a Lyapunov function V in W , then \bar{x} is stable. Moreover, if V is a strong Lyapunov function in W , then \bar{x} is locally asymptotically stable. If W is also bounded and forward invariant, we find $W \subseteq \mathcal{A}(\bar{x})$.*

Proof Before we start we introduce some notation and some elementary observations. Let $B_\varepsilon(\bar{x})$ denote the open ball around \bar{x} of radius ε . Let ε be small enough to guarantee $B_\varepsilon(\bar{x}) \subset W$ (which is possible as W is open). As $V(\bar{x}) = 0$, $V(x) > 0$ for $x \neq \bar{x}$, and V differentiable, we find $\alpha > 0$ s.t. $M_\alpha := \{x \in M \mid V(x) < \alpha\} \subset B_\varepsilon$. As $V(x(t))$ is in non-increasing in time and V constant on ∂M_α , the set M_α is forward invariant.

Now we proceed to the first claim. In order to prove stability, we have to show that for each $\varepsilon > 0$ there is a $\delta > 0$, s.t. a solution starting with a distance from \bar{x} smaller than δ will never have a distance larger ε . Without restriction, let ε be small enough s.t. $B_\varepsilon \subset M$. We know that we find an invariant set M_α contained in B_ε . As M_α is open, we find $B_\delta(\bar{x})$ contained in M_α . As M_α is invariant, all trajectories starting in $B_\delta(\bar{x})$ (and thus also in M_α) do not leave M_α , and thus do also not leave $B_\varepsilon(\bar{x})$.

We jump to the third claim: let us assume that W itself is bounded, forward invariant, and that V a strong Lyapunov function. Let us consider a trajectory $x(t)$ starting within W . As W is bounded, there is a sequence of time points $t_n \rightarrow \infty$ for that $(x(t_n))$ is converging, $x(t_n) \rightarrow y$. As V is strictly monotonously decreasing, $V(y) < V(x)$ for $x \neq \bar{x}$. Together with the invariance of W , this inequality implies $y \in W$. As $V(y) = \lim_{n \rightarrow \infty} V(x(t_n))$, we conclude that $(\text{grad } V(y))^* f(y) = 0$: if this equality is not true, we know that a trajectory $y(t)$, starting at the point y , has the property that $V(y) > V(y(\tau))$ for any fixed $\tau > 0$. Let t_{n_l} a subsequence of t_n s.t. $t_{n_l} > t_{n_l-1} + \tau$. Then, $V(x(t_{n_l})) \geq V(x(t_{n_l} + \tau)) \geq V(x(t_{n_l-1}))$. Passing to the limit $l \rightarrow \infty$, we find

$$V(y) \geq V(y(\tau)) \geq V(y),$$

and hence $V(y) = V(y(\tau))$, which leads to a contradiction if $(\text{grad } V(y))^* f(y) \neq 0$. This observation already implies that $y = \bar{x}$ and $x \in \mathcal{A}(\bar{x})$.

Last we return to the case of a general W (drop the condition that W is invariant). The introductory remark implies that there is a forward invariant, open neighbourhood M_α contained in M , and hence the argument above shows that all points within this neighbourhood asymptotically tend to \bar{x} . Therefore, \bar{x} is locally asymptotically stable. \square

The big advantage is that it is not necessary to solve the ODE. However, there is no general method how to find such a Lyapunov function – to construct such a function is an art not a technique.

This approach can be transferred into a more general background. Solutions can tend not only to fixed points, but to more “extended” objects, the ω -limit sets. We can generalise the concept of the Lyapunov function (interpreting f as generator of a flow on a manifold M):

Definition 2.31 (Lyapunov function II) Consider

$$\dot{x} = f(x).$$

The function $V : M \subset \mathbb{R}^n \rightarrow \mathbb{R}$ is called Lyapunov function for f , if

- (a) $V \in C^1(M, \mathbb{R})$
- (b) $V \geq 0$
- (c) $(\text{grad } V(x))^* f(x) \leq 0$ for all $x \in M$.

A quite famous theorem shows how useful these Lyapunov functions are:

Theorem 2.32 (LaSalle’s invariance principle) *If V is a Lyapunov function for a Lipschitz continuous function f in the sense of Definition 2.31, and $\Omega \subset M$ is a compact, positively invariant set, then*

$$\omega(p) \subseteq \{y \in \Omega \mid (\text{grad } V(y))^* f(y) = 0\} =: \mathcal{V}_0$$

for each $p \in \Omega$. Furthermore, $\omega(p)$ is contained in an invariant subset of \mathcal{V}_0 .

This allows to estimate a region where solutions will tend to, even if it is not possible to compute exactly a limit set. For a proof of this theorem and further reading see e.g. [119, 147].

2.3.2.3 Improved Predator Prey Model

As we have seen above, the basic Lotka Volterra predator prey model has some disadvantages; e.g. it shows up exponential growth of the prey if the predators are absent, and it is structurally unstable – this means, an arbitrary small perturbation of the right hand side will destroy most if not all of the periodic orbits. We can improve it by introducing the logistic growth term for the prey:

$$\dot{x} = ax \left(1 - \frac{x}{K}\right) - bxy \tag{2.8}$$

$$\dot{y} = cxy - dy. \tag{2.9}$$

The predators still are assumed to die out exponentially, if no prey is available, but the uptake of food (prey) is still proportional to the prey density.

As the model has a lot of parameters, it might make sense to reduce their number. This is done by rescaling: we introduce new variables for the populations and the time by $x = \alpha u$, $y = \beta v$, $t = \kappa \tau$, thus $\tau = \frac{t}{\kappa}$, the rescaled equations read:

$$\begin{aligned}\dot{x} &= \frac{dx}{dt} = \frac{d(\alpha u)}{dt} = \alpha \frac{du}{d\tau} \cdot \frac{d\tau}{dt} = \alpha \frac{du}{d\tau} \cdot \frac{1}{\kappa} \\ \dot{y} &= \frac{dy}{dt} = \frac{d(\beta v)}{dt} = \beta \frac{dv}{d\tau} \frac{d\tau}{dt} = \beta \frac{dv}{d\tau} \frac{1}{\kappa},\end{aligned}$$

thus,

$$\begin{aligned}\dot{u} &= \frac{\kappa}{\alpha} [a\alpha u(1 - \frac{\alpha u}{K}) - b\alpha u\beta v] = \kappa u(1 - \frac{\alpha u}{K}) - \kappa \beta buv \\ \dot{v} &= \frac{\kappa}{\beta} [c\alpha u\beta v - d\beta v] = \kappa c\alpha uv - \kappa dv.\end{aligned}$$

Now we define $\kappa = \frac{1}{a}$, $\alpha = \frac{d}{c}$, $\beta = \frac{a}{b}$ which simplifies the equations further:

$$\begin{aligned}\dot{u} &= a \cdot \frac{1}{a} u(1 - \frac{\frac{d}{c}u}{K}) - \frac{1}{a} \frac{a}{b} buv = u(1 - \frac{\frac{d}{c}u}{K}) - uv \\ \dot{v} &= \frac{1}{a} \frac{d}{c} uv - \frac{1}{a} dv = \frac{d}{a} uv - \frac{d}{a} v.\end{aligned}$$

Last, we introduce new parameters $\gamma = \frac{d}{a}$, $K' = \frac{c}{d}K$ (this simplifies the notation). By habit, we write the system again in variables x and y ; and for simplicity we write again K instead of K' . We furthermore only consider $\gamma = 1$; a more detailed analysis (which we do not perform) reveals, that for other values γ do not lead to a fundamental different behaviour. The result of these procedures is

$$\begin{aligned}\dot{x} &= x(1 - x/K) - xy \\ \dot{y} &= (x - 1)y.\end{aligned}$$

We obtained a vector field depending on one parameter only. There are three stationary points for the system (2.10):

$$P_0 = (0, 0), \quad P_1 = (K, 0), \quad P_2 = (1, 1 - \frac{1}{K}).$$

Obviously, P_2 does not have a biological meaning if $K < 1$. For $K = 1$ the points P_1 and P_2 “cross each other”. Note that we find a similar behaviour as in the Lotka-Volterra model with fishing. An increase of the energy available to the system (an increase of K) does by no means imply that the abundance of the prey becomes larger in case that predators are present. Only if the energy level is too small for predators, the number of prey linearly increases in K . At the moment the carrying

capacity is large enough for predators, they harvest all the surplus of the resources. Unexpectedly, not the prey but only the predator grows. All the energy in the system is transported through the levels of the food chain to the top predator. This is a principle we shall re-discover later, if we consider larger food chains. Though this is almost a paradox, it is falsely sometimes called the paradox of enrichment. The paradox of enrichment is defined below, when we consider an even more refined predator-prey model, the Rosenzweig model.

Now we investigate the stationary points using linearisation. The general Jacobian matrix reads

$$\begin{pmatrix} 1 - 2x/K - y & -x \\ y & x - 1 \end{pmatrix},$$

and yields for the stationary points:

- $(0, 0): \begin{pmatrix} 1 & 0 \\ 0 & -1 \end{pmatrix} \Rightarrow P_0$ is a saddle point

- $(K, 0): \begin{pmatrix} -1 & -K \\ 0 & K - 1 \end{pmatrix} \Rightarrow \lambda_1 = -1, \lambda_2 = K - 1$

If $K > 1$, then P_1 is a saddle point; if $K < 1$, P_1 is a stable node.

- $(1, 1 - 1/K): \begin{pmatrix} -1/K & -1 \\ 1 - \frac{1}{K} & 0 \end{pmatrix}$

The trace is $-1/K$ (negative in each case), the determinant is $1 - 1/K$ (with a change of sign at $K = 1$).

If $K > 1$, then P_2 is stable.

If $K < 1$, then P_2 is a saddle point.

It has to be checked, if there is a spiral or a node in the first case. The eigenvalues are

$$\lambda_{1,2} = -\frac{1}{2K} \pm \frac{1}{2} \sqrt{\left(\frac{1}{K}\right)^2 - 4\left(1 - \frac{1}{K}\right)}.$$

The discriminant is larger zero for small K , and changes sign if K becomes large. This change of sign happens at

$$\left(\frac{1}{K}\right)^2 + \frac{4}{K} - 4 = 0 \quad \Leftrightarrow \quad -4K^2 + 4K + 1 = 0 \quad \Leftrightarrow \quad K_{\pm} = \frac{1}{2}(1 \pm \sqrt{2})$$

As $K_- < 0$ and we only consider positive carrying capacities, this value does not play a role. If $1 < K \leq \frac{1}{2}(1 + \sqrt{2})$, then P_2 is a stable node (with two tangents for $K < \frac{1}{2}(1 + \sqrt{2})$ and one tangent for $K = \frac{1}{2}(1 + \sqrt{2})$). If $K > \frac{1}{2}(1 + \sqrt{2})$, then P_2 is a stable spiral.

In the next step, we apply the idea of Lyapunov functions to the improved predator prey model. Let $x > 0, y > 0$.

Case $K \geq 1$: As ansatz for a Lyapunov function, we choose $V(x, y) = x - \ln x + y - \left(1 - \frac{1}{K}\right) \ln y$. Thereby, we obtain

$$\begin{aligned}
 \frac{d}{dt}V(x, y) &= \left(1 - \frac{1}{x}\right)\dot{x} + \left(1 - \left(1 - \frac{1}{K}\right)\frac{1}{y}\right)\dot{y} \\
 &= \left(1 - \frac{1}{x}\right)\left(x\left(1 - \frac{x}{K}\right) - xy\right) + \left(1 - \left(1 - \frac{1}{K}\right)\frac{1}{y}\right)(x-1)y \\
 &= (x-1)\left(1 - \frac{x}{K} - y\right) + (x-1)y - \left(1 - \frac{1}{K}\right)(x-1) \\
 &= (x-1)\left(1 - \frac{x}{K}\right) - \left(1 - \frac{1}{K}\right)(x-1) \\
 &= -\frac{1}{K}(x-1)^2.
 \end{aligned}$$

The conditions for a Lyapunov function are satisfied:

1. Obviously, $V(x, y)$ is continuously differentiable for $x, y > 0$.
2. Due to $\ln x \leq x - 1$ we have $V(x, y) \geq 1$
3. $\frac{d}{dt}V(x, y) = -\frac{1}{K}(x-1)^2 \leq 0$

Here it is $\mathcal{V}_0 = \{(x, y) | \frac{d}{dt}V(x, y) = 0\} = \{(x, y) | x = 1, y > 0\}$. The only invariant subset of \mathcal{V}_0 is just the point $(1, 1 - 1/K)$, as in all other points, there is $\dot{x} \neq 0$ which leads to a contradiction. This means: All trajectories in $x > 0, y > 0$ converge towards the stationary point $(1, 1 - 1/K)$. A sketch of the qualitative behaviour in the phase plane can be found in Fig. 2.28.

Case $0 < K < 1$: Using

$$V(x, y) = x - \ln x + y,$$

as Lyapunov function, one can show convergence towards a stationary point also in this case.

Case $K \rightarrow \infty$: This limit case corresponds to the classical Volterra-Lotka model,

$$V(x, y) = x - \ln x + y - \ln y$$

which is here an invariant of motion (special case of a Lyapunov function). This means: The ω -limit set is a closed curve (already known), and corresponds to a periodic orbit.

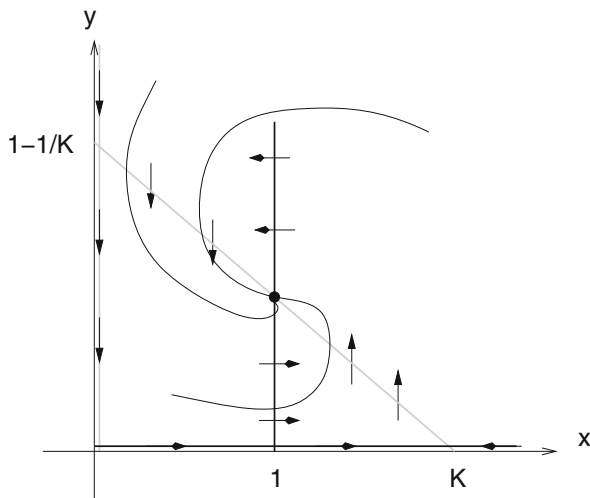


Fig. 2.28 Sketch of phaseplot of the improved predator prey model (2.8), (2.9); the $\dot{x} = 0$ isoclines are drawn as *grey lines*, the $\dot{y} = 0$ isoclines as *black lines*

2.3.2.4 Local Bifurcations in a Nutshell

As we have seen already, the qualitative behaviour (of a dynamical system) may depend on one (or several) parameters and change suddenly if a certain threshold is exceeded. E.g. stationary points may appear or disappear, they may change their stability and so on. Here, we introduce some elementary examples of such bifurcations, with one single parameter, the so-called bifurcations parameter (denoted by μ). I.e., we consider a system of differential equations $\dot{x} = f_\mu(x)$ where f not only depends on $x \in \mathbb{R}^n$ but also on a parameter $\mu \in \mathbb{R}$. Mostly, if we vary μ slightly, the behaviour of solutions will only change slightly and quantitatively, but not qualitatively. There are only some distinct values for μ in \mathbb{R} where we observe a qualitative change of the type mentioned above. These parameter values are called bifurcation points, and we say that the system undergoes a bifurcation at these parameter points. Fortunately, our applications only require the understanding of a very limited number of such bifurcations. Moreover, the bifurcations we will meet can be very well characterised. We sketch them below. Of course, there is an unlimited number of bifurcation types, and also for those bifurcation we describe below a lot of details is left out. More information about bifurcation theory can be found e.g. in [6, 98, 156].

Saddle-Node Bifurcation

From “nothing” there appears a saddle and a node (this kind of bifurcation is also called “blue sky bifurcation” which also self-explanatory).

We consider a simple, prototypical 1D example

$$\dot{x} = \mu - x^2 =: f_\mu(x), \quad (2.10)$$

Fig. 2.29 Graphs for the right hand side of (2.10), the existence/position of positive roots depends on the bifurcation parameter μ . Graph 1: there are no stationary points, graph 2: there is one stationary point (hybrid), graph 3: there is one stable and one unstable stationary point

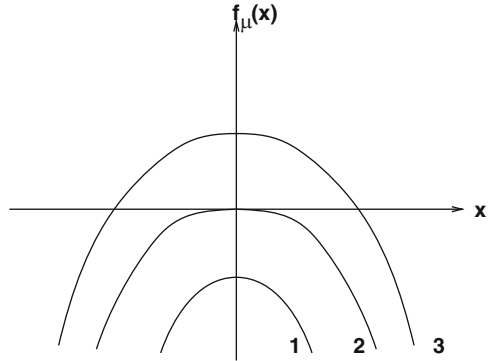
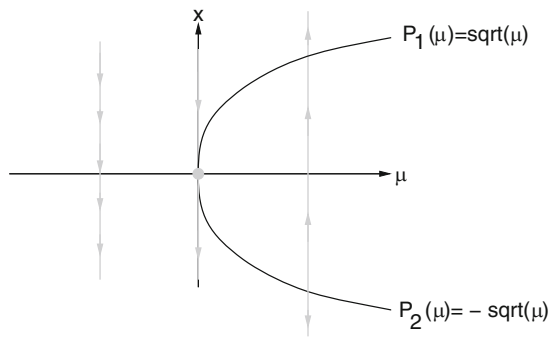


Fig. 2.30 Bifurcation diagram for the saddle node bifurcation (2.10)



see Fig. 2.29 for the graph. The bifurcation diagram is sketched in Fig. 2.30. We observe: If the parameter μ varies, then for $\mu < 0$ there are no singularities, for $\mu = 0$ there is exactly one stationary point, and for $\mu > 0$ appears a pair of stationary points, one of them is stable, the other one is unstable.

2D case:

$$\begin{cases} \dot{x} = \mu - x^2 \\ \dot{y} = -y \end{cases} \quad (2.11)$$

(thus, the bifurcation parameter does not concern the variable y , only x). In the phase plane, different qualitative behaviour appears, dependent on μ , see Fig. 2.31. The general Jacobian is

$$J_f(x, y) = \begin{pmatrix} -2x & 0 \\ 0 & -1 \end{pmatrix},$$

this yields for the two stationary points in the last case:

$$J_f(\sqrt{\mu}, 0) = \begin{pmatrix} -2\sqrt{\mu} & 0 \\ 0 & -1 \end{pmatrix}, \quad J_f(-\sqrt{\mu}, 0) = \begin{pmatrix} 2\sqrt{\mu} & 0 \\ 0 & -1 \end{pmatrix}$$

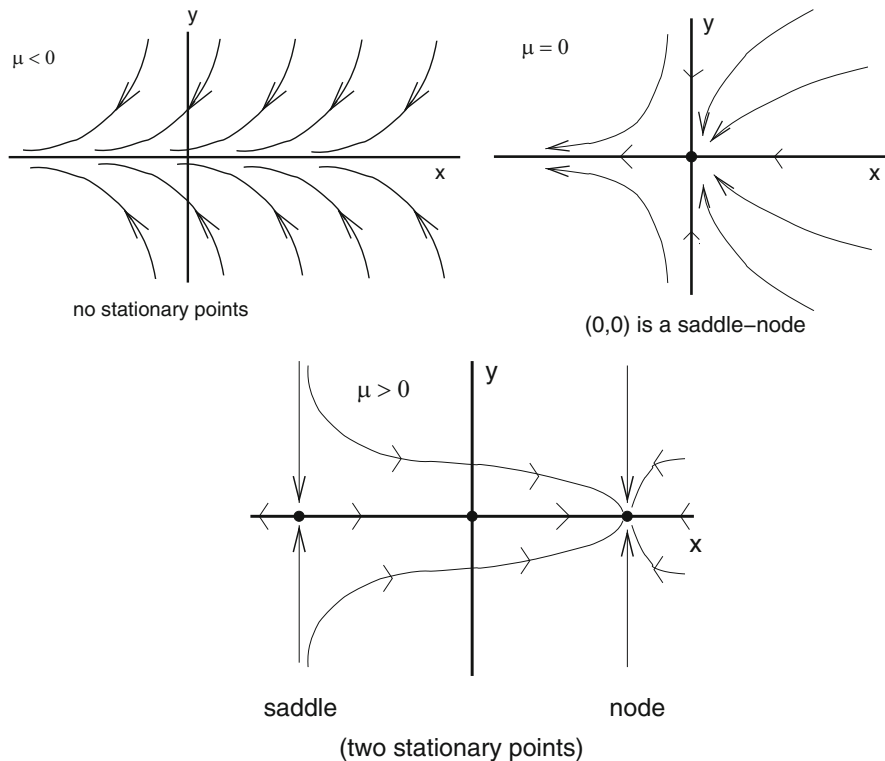


Fig. 2.31 Phase plane for the 2D example of a saddle node bifurcation (2.11)

Transcritical Bifurcation (Exchange of stability)

Two stationary points exchange their stability, exactly at the parameter value, where both points meet.

Again, we consider a 1D example first:

$$\dot{x} = \mu x - x^2 = x(\mu - x) = f_\mu(x). \quad (2.12)$$

The position of the “peak” can be computed:

$$f'_\mu(x) = 0 \Leftrightarrow \mu - 2x = 0 \Leftrightarrow x = \frac{\mu}{2},$$

$$\leadsto f_\mu\left(\frac{\mu}{2}\right) = \frac{\mu^2}{4},$$

thus, the peak has the coordinates $\left(\frac{\mu}{2}, \frac{\mu^2}{4}\right)$, which is on a parabola, dependent on μ .

Fig. 2.32 Graphs for the right hand side of (2.12)

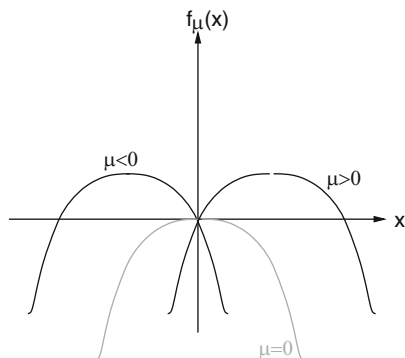
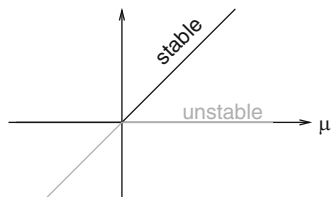


Fig. 2.33 Bifurcation diagram for the transcritical bifurcation (2.12)



For $\mu < 0$, 0 is stable, μ is unstable.

For $\mu = 0$, $0 = \mu$ is hybrid (unstable).

For $\mu > 0$, 0 is unstable, μ is stable.

Observation (see also Fig. 2.32): Two stationary points exchange their stability depending on the parameter μ , at the parameter value where they meet. For the bifurcation diagram, see Fig. 2.33. Again, the bifurcation parameter only affects the variable x . In the 2D case,

$$\begin{cases} \dot{x} = \mu x - x^2 \\ \dot{y} = -y \end{cases} \rightsquigarrow J(x, y) = \begin{pmatrix} \mu - 2x & 0 \\ 0 & -1 \end{pmatrix},$$

the phase plane looks like Fig. 2.34, dependent on the chosen μ .

Pitchfork Bifurcation

A stationary point is stable for parameter values $\mu \leq \mu_0$, for $\mu > \mu_0$ there show up two additional stationary points which are stable, whereas the originally stable point becomes unstable.

First, we consider the 1D example

$$\begin{aligned} \dot{x} &= \mu x - x^3 = x(\mu - x^2) \\ & (= x(x + \sqrt{\mu})(x - \sqrt{\mu}) \quad \text{for } \mu \geq 0) \end{aligned} \tag{2.13}$$

For $\mu < 0$, 0 is stable and the only stationary point.

For $\mu = 0$, 0 is stable and the only stationary point.

For $\mu > 0$, 0 is unstable, $\sqrt{\mu}$ and $-\sqrt{\mu}$ are stable.

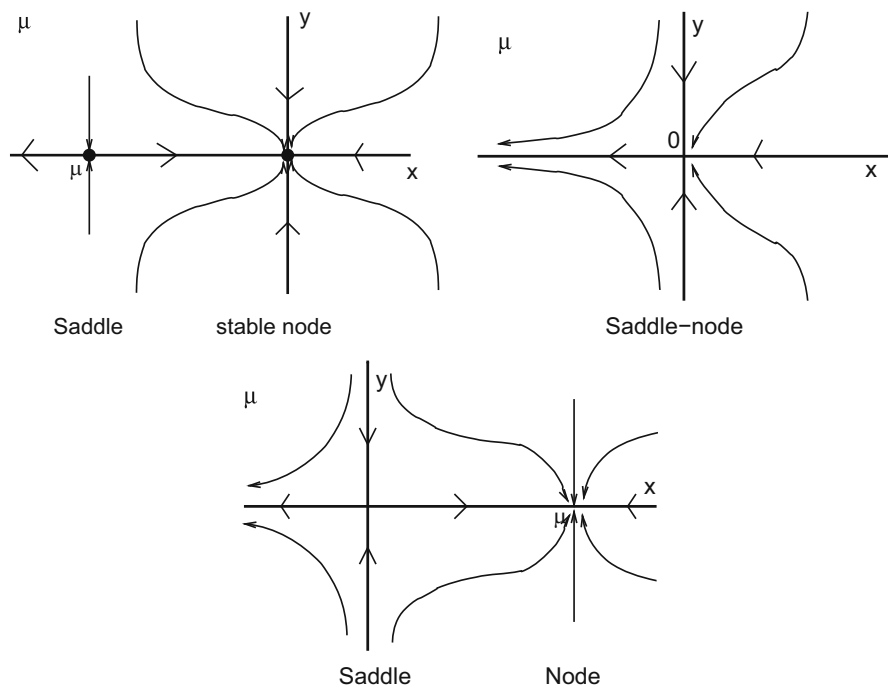


Fig. 2.34 Phase plane for the 2D example of a transcritical bifurcation

The graphs can be seen in Fig. 2.35, the bifurcation diagram in Fig. 2.36. You can see: it looks like a pitchfork! A typical 2D example is

$$\begin{cases} \dot{x} = \mu x - x^3 \\ \dot{y} = -y \end{cases}$$

(μ is only involved in the equation of the variable x), for the phase plane behaviour see Fig. 2.37.

Hopf Bifurcation

Roughly speaking: A stationary point loses its stability, at the same time a stable periodic orbit shows up around the stationary point. Since periodic orbits cannot show up in the (continuous!) autonomous 1D case, 2D is the simplest case allowing for such a behaviour.

(a) Supercritical case:

Let $\mu \in \mathbb{R}$ and consider as an example

$$\begin{cases} \dot{x} = -y + x(\mu - x^2 - y^2) \\ \dot{y} = x + y(\mu - x^2 - y^2) \end{cases} =: f_\mu(x, y). \quad (2.14)$$

Fig. 2.35 Graphs for the right hand side of (2.13)

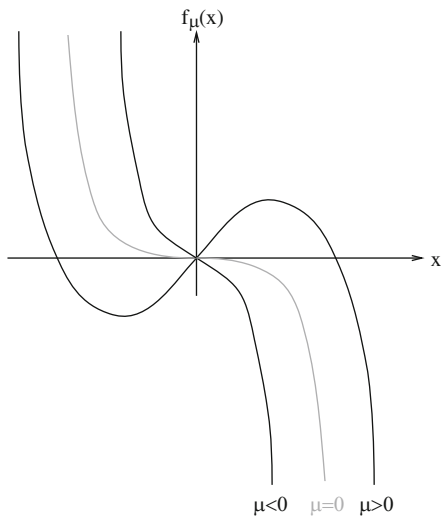
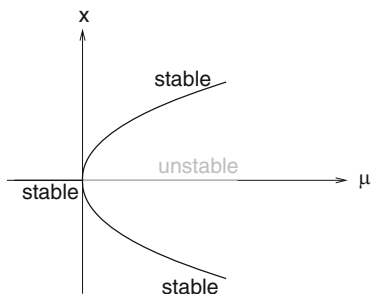


Fig. 2.36 Bifurcation diagram for the pitchfork bifurcation



$P_0 = (0, 0)$ is the only stationary point, the Jacobian matrix reads

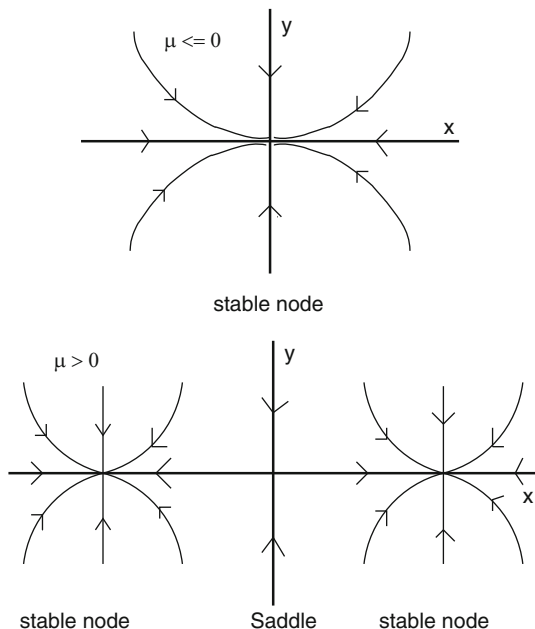
$$J_{f,\mu}(0, 0) = \begin{pmatrix} \mu & -1 \\ 1 & \mu \end{pmatrix},$$

with trace $tr = 2\mu$, determinant $det = \mu^2 + 1$ and discriminant $\Delta = -4$. We introduce the function $V(x, y) = \frac{1}{2}(x^2 + y^2)$ that basically measures the distance of a point to the origin. Along solutions it is

$$\begin{aligned} \dot{V}(x, y) &= \frac{\partial V}{\partial x} \dot{x} + \frac{\partial V}{\partial y} \dot{y} \\ &= x(-y + x(\mu - x^2 - y^2)) + y(x + y(\mu - x^2 - y^2)) \\ &= (x^2 + y^2)(\mu - x^2 - y^2). \end{aligned}$$

If $\mu \leq 0$ then P_0 is globally asymptotically stable.

Fig. 2.37 Phase plane for the 2D example of a pitchfork bifurcation



If $\mu > 0$ then P_0 is a “repellor”; since in $\{(x, y) \mid x^2 + y^2 < \mu\}$ we have $\dot{V} > 0$ for $(x, y) \neq (0, 0)$. Furthermore, $\{(x, y) \mid x^2 + y^2 = \mu\}$ is the trace of a periodic orbit ζ_μ , because f_μ is tangential to the circle $\{(x, y) \mid x^2 + y^2 = \mu\}$: $(x, y)f_\mu(x, y) = 0$.

ζ_μ is orbitally stable, since outside of ζ_μ it is $\dot{V} < 0$, inside $\dot{V} > 0$ for $(x, y) \neq (0, 0)$. (Orbital stability is a kind of generalisation of the “usual” stability; the difference is that in the orbital stability, the distance between a solution and the complete orbit/trajectory/solution curve is considered – instead of comparing the positions of the solutions at a certain time point. This plays especially a role for periodic orbits, where the period may differ, even though the orbits are nearby.)

For $\mu \rightarrow 0+$, ζ_μ shrinks itself to P_0 . Figure 2.38 shows the corresponding bifurcation diagram, and the qualitative behaviour of the solutions in the phase plane can be seen in Fig. 2.39. Mathematical interpretation: If the sign of μ changes from negative to positive, a pair of conjugate complex eigenvalues $\lambda_{1,2}(\mu) = \mu \pm i$ crosses the imaginary axis from the left halfspace to the right.

More generally: A supercritical Hopf bifurcation means that a pair of conjugate complex eigenvalues of the Jacobian of a stationary point crosses the imaginary axis from left to right at a certain parameter value μ_0 . There, the stationary point loses its stability and stable periodic orbits appear (limit cycles).

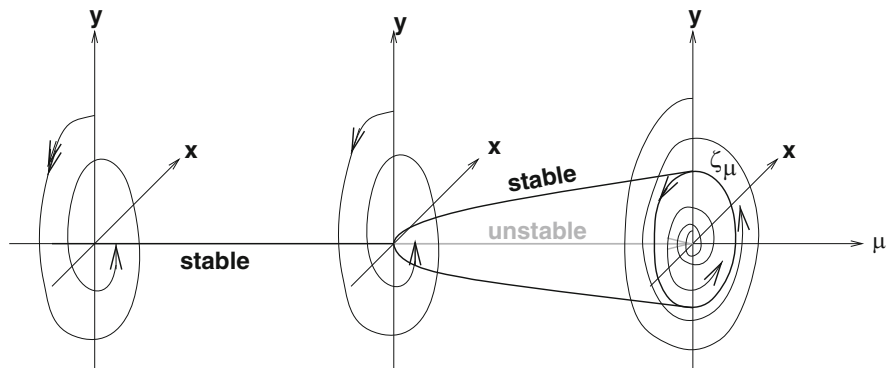


Fig. 2.38 Bifurcation diagram for the supercritical Hopf bifurcation (2.14)

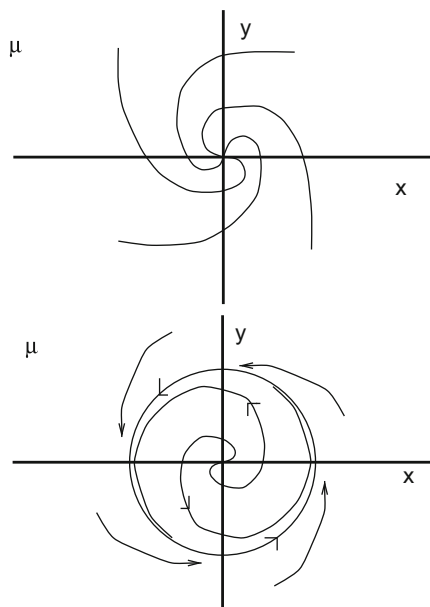


Fig. 2.39 Qualitative behaviour of the solutions in the phase plane in case of a supercritical Hopf bifurcation (2.14)

- (b) Subcritical case: Invert the time course and the “direction” of the parameter ($v := -\mu$) in the example above (supercritical case):

$$\begin{aligned}\dot{x} &= y + x(v + x^2 + y^2) \\ \dot{y} &= -x + y(v + x^2 + y^2).\end{aligned}\tag{2.15}$$

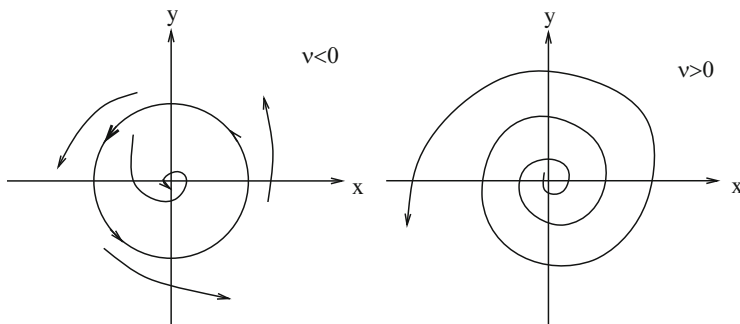


Fig. 2.40 Qualitative behaviour of the solutions in the phase plane in case of a subcritical Hopf bifurcation (2.15)

For $v \geq 0$ P_0 is a repeller. For $v < 0$ P_0 is a local attractor with

$$\{(x, y) \mid x^2 + y^2 < |v|\} = \mathcal{A}(P_0)$$

(this can be shown by the same Lyapunov function as above).

ζ_v is a orbitally unstable periodic orbit, see Fig. 2.40. In general: In the case of a subcritical Hopf Bifurcation a pair of conjugate complex eigenvalues of the Jacobian of a stationary point crosses the imaginary axis from left to right for a certain parameter value v_0 . Then, the stationary point loses its stability, for $v < v_0$ there exist orbitally unstable periodic orbits which shrink themselves to the stationary point in the case of $v \rightarrow v_0$ (an example is the Lorenz equation, see [98]).

The following famous theorem (see e.g. [98] for more details) can be applied to show the existence of periodic orbits via a Hopf bifurcation.

Theorem 2.33 (Hopf [125]) Consider the system $\dot{x} = f_\mu(x)$, $x \in \mathbb{R}^n$ and assume that f_{μ_0} has an equilibrium at (x_0, μ_0) with the following properties:

The Jacobian $f'_{\mu_0}(x_0)$ has exactly one pair of purely imaginary complex eigenvalues (no other eigenvalues with real parts = 0). We call this point in the parameter space a Hopf point.

Then there is a (locally) smooth curve of equilibria $(x(\mu), \mu)$ with $x(\mu_0) = x_0$. The eigenvalues $\lambda(\mu)$, $\bar{\lambda}(\mu)$ of the Jacobian $f'_\mu(x(\mu))$ which are purely imaginary at $\mu = \mu_0$, depend smoothly on μ .

If additionally the condition

$$\frac{d}{d\mu}(\operatorname{Re} \lambda(\mu))|_{\mu=\mu_0} =: d \neq 0$$

is satisfied, then there exists a unique three-dimensional so-called “centre manifold”. This manifold passes through (x_0, μ_0) in $\mathbb{R}^n \times \mathbb{R}$ and a smooth system of

coordinates (preserving the planes $\mu = \text{const.}$), such that the differential equation can be formulated on the surface corresponding to the eigendirections of the pair of purely imaginary eigenvalues (depending on $(x, \mu) \in \mathbb{R}^n \times \mathbb{R}$) as

$$\begin{aligned}\dot{x}_1 &= (d\mu + a(x_1^2 + x_2^2))x_1 - (\omega + c\mu + b(x_1^2 + x_2^2))x_2 + \text{higher order terms} \\ \dot{x}_2 &= (\omega + c\mu + b(x_1^2 + x_2^2))x_1 + (d\mu + a(x_1^2 + x_2^2))x_2 + \text{higher order terms},\end{aligned}$$

If $a \neq 0$ is satisfied, then a surface of periodic solutions in the centre manifold exists which has quadratic tangency with the eigenspace of $\lambda(\mu_0)$, $\bar{\lambda}(\mu_0)$ (the surface agrees to second order with the paraboloid $\mu = -(a/d)(x^2 + y^2)$).

If $a < 0$, then the periodic solutions are stable limit cycles; if $a > 0$, then the periodic orbits are repelling (i.e., unstable).

We will apply this theorem for several models.

2.3.2.5 Routh-Hurwitz Criteria

We are looking for a simple possibility to check the stability of stationary points, especially in higher-dimensional systems, where it may not be so easy to compute the eigenvalues explicitly. Let us start with the (normalised) characteristic polynomial (originating e.g. from a Jacobian matrix),

$$\lambda^k + a_1\lambda^{k-1} + a_2\lambda^{k-2} + \dots + a_k = 0.$$

The Routh-Hurwitz Criteria [196] do not yield information about the eigenvalues themselves, but about the sign of their real part – and this is sufficient to decide about stability of a stationary point in case we consider an ODE. For $k = 2$, we already know the criterion based on determinant and trace. This criterion is generalised to $k > 2$. Of course, more conditions come in. First, some “auxiliary” matrices are defined:

$$\begin{aligned}H_1 &= (a_1), & H_2 &= \begin{pmatrix} a_1 & 1 \\ a_3 & a_2 \end{pmatrix}, & H_3 &= \begin{pmatrix} a_1 & 1 & 0 \\ a_3 & a_2 & a_1 \\ a_5 & a_4 & a_3 \end{pmatrix}, \dots \\ H_j &= \begin{pmatrix} a_1 & 1 & 0 & 0 & \dots & 0 \\ a_3 & a_2 & a_1 & 1 & \dots & 0 \\ a_5 & a_4 & a_3 & a_2 & \dots & 0 \\ \vdots & \vdots & \vdots & \vdots & & \vdots \\ a_{2j-1} & a_{2j-2} & a_{2j-3} & a_{2j-4} & \dots & a_j \end{pmatrix}, & \dots & H_k = \begin{pmatrix} a_1 & 1 & 0 & \dots & 0 \\ a_3 & a_2 & a_1 & \dots & 0 \\ \vdots & \vdots & \vdots & & \vdots \\ 0 & 0 & \dots & & a_k \end{pmatrix},\end{aligned}$$

i.e., the (l, m) term in the matrix H_j is given by

$$\begin{aligned} a_{2j-m} & \text{ for } 0 < 2l - m \leq k \\ 1 & \text{ for } 2l = m \\ 0 & \text{ for } 2l < m \text{ or } 2l > k + m. \end{aligned}$$

All eigenvalues have negative real parts if and only if the determinants of H_j (called Hurwitz matrices) are positive, i.e.,

$$\det H_j > 0, \quad j = 1, 2, \dots, k.$$

It is possible to formulate these conditions in more simple terms for $k = 2, \dots, 5$:

$$k = 2 : a_1 > 0, \quad a_2 > 0$$

$$k = 3 : a_1 > 0, \quad a_3 > 0, \quad a_1 a_2 > a_3$$

$$k = 4 : a_1 > 0, \quad a_3 > 0, \quad a_4 > 0, \quad a_1 a_2 a_3 > a_3^2 + a_1^2 a_4$$

$$k = 5 : a_i > 0 \ (i = 1 \dots 5), \quad a_1 a_2 a_3 > a_3^2 + a_1^2 a_4,$$

$$(a_1 a_4 - a_5)(a_1 a_2 a_3 - a_3^2 - a_1^2 a_4) > a_5(a_1 a_2 - a_3)^2 + a_1 a_5^2.$$

These conditions are really easy to apply in many cases and thus provide a useful tool a stability check.

2.3.2.6 Different Types of Functional Responses

The improved predator prey model (2.8), (2.9) showed nice results, but no stable limit cycles. But such oscillatory solutions are often observed – how to find suitable models which show up this effect?

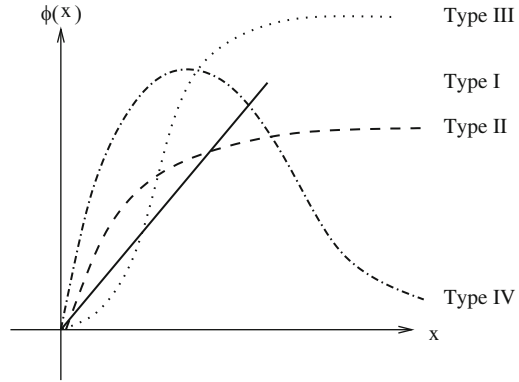
Idea: Choose a more realistic “functional response”, i.e., the rate at which each predator captures prey – instead of a linearly increasing function of prey density (as a direct consequence of the law of mass action), there must be a kind of “saturation” (the predators cannot eat unlimited amounts of food at once, catching and consuming needs some time etc.)

Typically, one distinguishes four different types of functional responses [152] (see Fig. 2.41 for comparison):

Type I: The number of prey which is eaten per predator per unit time (also called the “intake rate”) depends linearly on the prey density (possibly with a fixed maximum). Typical approach:

$$\Phi(x) = cx,$$

Fig. 2.41 Four typical types of functional responses: Type I (solid line), Type II (dashed line), Type III (dotted line), Type IV (dash-dotted line)



as chosen in the Lotka-Volterra predator prey model, and also in the “improved” predator prey model.

Type II: The intake rate decelerates and approaches a maximum (i.e., saturation of the food uptake), because the predators need time to handle the prey and eat it up. Typical approach:

$$\Phi(x) = \frac{cx}{\alpha + x}.$$

Type III: Similar to type II, but for low prey densities, it increases slower than linear at small prey densities (e.g. the prey is very shy at small densities; at higher densities they may form larger flocks that are more easily hunted; the predators have to learn how to catch the prey). Typical approach:

$$\Phi(x) = \frac{cx^2}{\alpha^2 + x^2}.$$

Type IV: For high prey densities, the per capita predation rate decreases (e.g. due to prey interference or prey toxicity). Typical approach:

$$\Phi(x) = \frac{cx}{\frac{x^2}{i} + x + a},$$

where $c, i, a > 0$ are constant.

For the example of the typical type II functional response, we have a short look on how to find a suitable function.

Idea: It takes some time to handle the prey, let T_h denote the handling time (for one prey item) and V the number of prey items, which are attacked. T is the total time, x the number of prey. One assumes that the number of caught prey is proportional to the potential prey population and also to the total available searching

time. This leads to the following approach:

$$V = a(T - T_h V)x,$$

where a , the proportionality constant, is called the searching efficiency or attack rate. We solve this equation for V and get

$$V = \frac{aTx}{1 + aT_h x},$$

which can be rewritten as $\phi(x) = \frac{cN}{a+N}$. This equation is called “Holling’s disk equation”, as it was originally introduced by C.S. Holling for an artificial experiment, where sandpaper discs had to be searched by “predators” [122].

Note that this function resembles very much the Monod equation respectively the Michaelis-Menten equation, which will be introduced later in a different context.

A nice real-world example for a functional response of Type II can be found in [36], where barren-ground caribous were observed which are hunted by wolves.

2.3.2.7 Rosenzweig-MacArthur Predator Prey Model

In this subsection, we consider a predator prey model with a functional response type II, according to Rosenzweig-MacArthur [205]. The ODE system reads:

$$\begin{aligned}\frac{dx}{dt} &= rx \left(1 - \frac{x}{K}\right) - \frac{cxy}{a + x} \\ \frac{dy}{dt} &= \frac{bxy}{a + x} - my.\end{aligned}$$

Reparametrisation helps to simplify the system slightly. Choose the new variables $\tilde{x} = \frac{x}{a}$, $\tilde{y} = \frac{c}{ar}y$ and $\tilde{t} = rt$; but omitting the tildes again yields:

$$\begin{aligned}\frac{dx}{dt} &= x \left(1 - \frac{x}{\gamma}\right) - \frac{xy}{1 + x} \\ \frac{dy}{dt} &= \beta \left(\frac{x}{1 + x} - \alpha\right) y,\end{aligned}$$

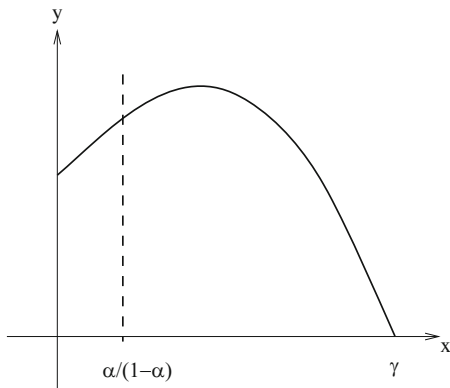
where $\alpha = \frac{m}{b}$, $\beta = \frac{b}{r}$, $\gamma = \frac{K}{a}$. There are three stationary points, resulting from the intersection points of the isoclines (see Fig. 2.42):

$$(x_0, y_0) = (0, 0)$$

$$(x_1, y_1) = (\gamma, 0)$$

$$(x_2, y_2) = \left(x^*, (1 + x^*)\left(1 - \frac{x^*}{\gamma}\right)\right), \quad \text{where } x^* = \frac{\alpha}{1 - \alpha}.$$

Fig. 2.42 The (nontrivial) isoclines of the Rosenzweig predator prey model: $\dot{x} = 0$ solid line, $\dot{y} = 0$ dashed line



Next, we rewrite the rescaled differential equations as

$$\begin{aligned}\frac{dx}{dt} &= f(x)(g(x) - y) \\ \frac{dy}{dt} &= \beta(f(x) - \alpha)y,\end{aligned}$$

where

$$f(x) = \frac{x}{1+x}, \quad g(x) = (1+x) \left(1 - \frac{x}{\gamma}\right).$$

Note that $f(x^*) - \alpha = 0$ and $g(x^*) = x^*$. With this trick, the Jacobian matrix is quite easy to write:

$$J = \begin{pmatrix} f(x)g'(x) + f'(x)g(x) - yf'(x) & -f(x) \\ \beta f'(x)y & \beta(f(x) - \alpha) \end{pmatrix}.$$

Now we can check the eigenvalues of the Jacobian matrix in the stationary points:

In $(0, 0)$:

$$J = \begin{pmatrix} 1 & 0 \\ 0 & -\alpha\beta \end{pmatrix},$$

with the eigenvalues $\lambda_1 = 1$, $\lambda_2 = -\alpha\beta \rightsquigarrow$ saddle point.

In $(\gamma, 0)$: Obviously $g(\gamma) = 0$, then the Jacobian matrix reads:

$$J = \begin{pmatrix} -1 & -f(\gamma) \\ 0 & \beta(f(\gamma) - \alpha) \end{pmatrix},$$

with the eigenvalues $\lambda_1 = -1$, $\lambda_2 = \beta \left(\frac{\gamma}{1+\gamma} - \alpha \right)$. Thus, this equilibrium is stable (a node) if

$$f(\gamma) = \frac{\gamma}{1+\gamma} < \alpha \quad \Leftrightarrow \quad x^* = \frac{\alpha}{1-\alpha} > \gamma,$$

otherwise a saddle point.

In $(x^*, g(x^*))$: Then, the Jacobian matrix reads:

$$J = \begin{pmatrix} \alpha g'(x^*) & -\alpha \\ \beta f'(x^*)g(x^*) & 0 \end{pmatrix}.$$

The corresponding characteristic equation is

$$\lambda^2 - \alpha g'(x)\lambda + \alpha\beta f'(x^*)g(x^*) = 0.$$

We can use the Routh-Hurwitz criteria (see Sect. 2.3.2.5) to check for stability: For the case $n = 2$, we need both coefficients to be > 0 . The constants α and β satisfy this condition; also $f'(x)$ is strictly positive. In case of $-1 < x^* < \gamma$ the $g(x^*)$ is also positive (this is satisfied if the coexistence point is in the positive area). All in all, this means: the stability of the coexistence point (equilibrium) depends on the sign of $g'(x^*)$:

If $g'(x^*) < 0$, then the coexistence point is stable.

If $g'(x^*) > 0$, then the coexistence point is unstable.

Note that the eigenvalues are purely imaginary, if $g'(x^*) = 0$. We find here the situation of a Hopf bifurcation! We expect (at least) one stable periodic orbit to show up.

Let us consider the dependency of the carrying capacity of the prey, K : If K increases (which is corresponding to an increasing dimensionless parameter γ), then the isocline of the prey, and its peak, is moved to the right.

Remark $g'(x^*)$ corresponds to the slope of the isocline of the prey, at that point where it intersects the isocline of the predators. The region, where this slope is larger zero is also increased, when K is increased. Thus, increasing K to sufficiently large values, destabilises the coexistence point (i.e., the coexistence point loses its stability and a stable periodic orbit shows up; by Hopf bifurcation, see Fig. 2.43). The oscillations may become this large, that the periodic orbit comes close to the axes, this is, the population size becomes temporally (in a periodic manner) small. In this situation, noise may drive one of the species to extinction. This phenomenon is called the “paradox of enrichment”, which means: increasing the capacity of an ecosystem may destabilise the whole system. Thus, be careful in enriching ecosystems!

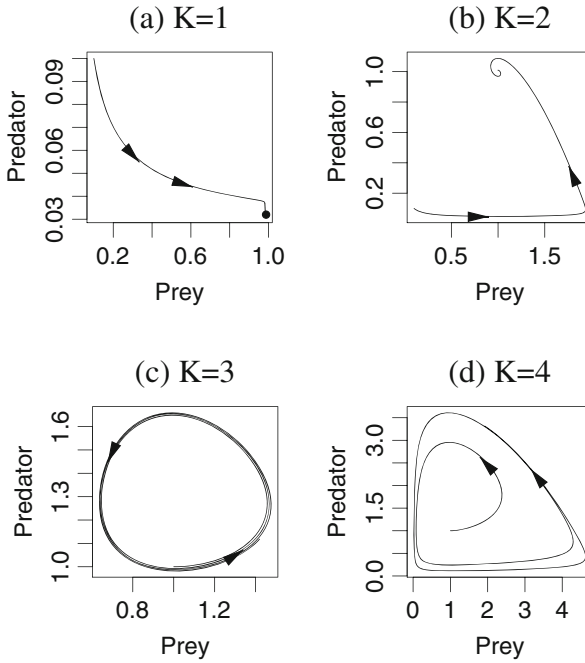


Fig. 2.43 Paradox of enrichment: increasing K leads to an oscillatory destabilisation of the previously stable coexistence point (**a**, indicated by the *black dot*) in an oscillatory manner (**b**), (**c**). These oscillations increase with K (**c**), (**d**) until they get close to the axes. Stochastic perturbation will lead to an extinction of the predator or even of both species

2.3.2.8 Freedman Wolkowicz Predator Prey Model

A typical example for a functional response of type IV, as mentioned already above, is the model of Freedman and Wolkowicz,

$$\begin{aligned}\dot{x} &= rx \left(1 - \frac{x}{K}\right) - \frac{cx}{\frac{x^2}{i} + x + a} y \\ \dot{y} &= \frac{bcx}{\frac{x^2}{i} + x + a} y - my\end{aligned}$$

Without going into the details here, we mention shortly that this model may exhibit two coexistence points under certain conditions for the parameters, and further interesting phenomena, as a global bifurcation (a homoclinic orbit appears). In opposite to local bifurcations, a global bifurcation affects the whole system. For more details to this model, see e.g. [152] or [74].

2.3.2.9 Stability of Time-Discrete, Nonlinear Systems

Again, linearisation is a useful approach to get information about the qualitative behaviour of nonlinear systems. Analogously to the time-continuous case, one can formulate a stability statement as follows:

Theorem 2.34 *Let $x_{n+1} = f(x_n)$ be an autonomous, time-discrete dynamical system. Suppose $f : D \rightarrow D, D \subseteq \mathbb{R}^m$ open, is twice continuously differentiable in some neighbourhood of a fixed point $\bar{x} \in D$. Let J be the Jacobian matrix of f , evaluated at \bar{x} . Then it holds:*

1. \bar{x} is asymptotically stable if all eigenvalues of J have absolute value less than 1.
2. \bar{x} is unstable if at least one eigenvalue of J has absolute value greater than 1.

The proof can be transferred easily from the 1D case and thus is omitted here.

Remark 2.35 If $\max\{|\lambda| : \lambda \text{ eigenvalue of } K\} = 1$, we cannot give a statement about the stability of the fixed point \bar{x} by that criterion; the behaviour depends on higher order terms.

Recall that in two dimensions, the condition for stability can be rewritten as (see Proposition 1.27)

$$2 > 1 + \det(J) > |\operatorname{tr}(J)|.$$

2.3.2.10 Host-Parasitoid Systems

We consider a system of two insect species, both have several life-cycle stages including eggs, larvae, pupae and adults (following the approach in [26, 42, 58]). Insect populations can easily be divided into discrete generations, so it makes sense to use discrete models in this case. One of the two species, the so-called parasitoid, exploits the second as follows: An adult female parasitoid looks for a host, on which it deposits its eggs (there are several possibilities to do that: attaching to the outer surface of the larvae or pupae of the host, or injection into the host's flesh). These eggs develop to larval parasitoids which grow at the expense of their host, even it is possible, that the host is killed by that. Obviously, the life-cycles of these two species are coupled to some extent, we assume the following properties for a simple model for this system:

1. Parasitised hosts give rise to the next generation of the parasitoid species.
2. Non-parasitised hosts give rise to the next generation of their own species.
3. The fraction of parasitised hosts depends on one or both population densities.

At the moment, we neglect natural mortality in order to put up the basic host-parasitoid model. The following definitions are used:

x_n = Host species density in generation n

P_n = Parasitoid density in generation n

$f = f(x_n, P_n)$ = Fraction of non-parasitised hosts

λ = Host reproductive number

c = Average number of viable eggs that a parasitoid puts on a single host

By these assumptions we come to the following basic host-parasitoid model:

$$x_{n+1} = \lambda x_n f(x_n, P_n)$$

$$P_{n+1} = cx_n(1 - f(x_n, P_n)).$$

One special case and famous example for such a host-parasitoid model is the Nicholson-Bailey model. They made the following assumptions for their modelling approach:

- The encounters of host and parasitoid happen randomly, thus the number of encounters N_e is proportional to the product of their densities,

$$N_e = ax_n P_n$$

where a is the so-called searching efficiency of the parasitoid (this assumption is due to the law of mass action).

- The first encounter is the relevant one; further encounters do not increase or decrease the number of eggs etc.

Thus, one has to distinguish between hosts, which had no encounter, and hosts with r encounters, where $r \geq 1$. The probability of r encounters can be represented by a probability distribution which is based on the average number of encounters per unit time. Here, the Poisson distribution is the appropriate one which leads to

$$f(x_n, P_n) = p(0) = e^{-aP_n}$$

(the zero term of the Poisson distribution corresponds to the fraction without parasitoids). This reasoning yields the Nicholson-Bailey equations:

$$x_{n+1} = \lambda x_n e^{-aP_n}$$

$$P_{n+1} = cx_n(1 - e^{-aP_n}).$$

Next step is to analyse the system. Let

$$F(x, P) = \lambda x e^{-aP}$$

$$G(x, P) = cx(1 - e^{-aP}).$$

Stationary solutions are

- The trivial one: $x = 0$ (then in the next step, also $P = 0$ is reached, independent of the initial value)
- $\bar{x} = \lambda \bar{x} e^{-a\bar{P}}$, $\bar{P} = c\bar{x}(1 - e^{-a\bar{P}})$
 $\Leftrightarrow \bar{P} = \frac{\ln \lambda}{a}$, $\bar{x} = \frac{\lambda \ln \lambda}{(\lambda - 1)ac}$
 Only for $\lambda > 1$, \bar{P} is positive (and biologically meaningful)

The Jacobian reads

$$\begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} = \begin{pmatrix} \frac{\partial F(\bar{x}, \bar{P})}{\partial x} & \frac{\partial F(\bar{x}, \bar{P})}{\partial P} \\ \frac{\partial G(\bar{x}, \bar{P})}{\partial x} & \frac{\partial G(\bar{x}, \bar{P})}{\partial P} \end{pmatrix} = \begin{pmatrix} \lambda e^{-a\bar{P}} & -a\lambda \bar{x} e^{-a\bar{P}} \\ c(1 - e^{-a\bar{P}}) & ca\bar{x} e^{-a\bar{P}} \end{pmatrix} = \begin{pmatrix} 1 & -a\bar{x} \\ c(1 - \frac{1}{\lambda}) & \frac{ca}{\lambda} \bar{x} \end{pmatrix}.$$

The trace and the determinant of this matrix are computed as follows:

$$\begin{aligned} \text{tr } J &= 1 + \frac{ca}{\lambda} \bar{x} = 1 + \frac{\ln \lambda}{\lambda - 1}, \\ \det J &= \frac{ca}{\lambda} \bar{x} + ca\bar{x}(1 - \frac{1}{\lambda}) = ca\bar{x} = \frac{\lambda \ln \lambda}{\lambda - 1}. \end{aligned}$$

Now, we want to show that $\det J > 1$. Equivalently, one can show that $S(\lambda) = \lambda - 1 - \lambda \ln \lambda < 0$. This function $S(\lambda)$ has the following properties: $S(1) = 0$, $S'(\lambda) = 1 - \ln \lambda - \lambda \frac{1}{\lambda} = -\ln \lambda$. Thus, for $\lambda \geq 1$ it is $S'(\lambda) < 0$ and $S(\lambda)$ is a decreasing function of λ . Consequently, for $\lambda \geq 1$ it is $S(\lambda) < 0$ which is equivalent to $\det J > 1$. But in this case, at least one eigenvalue has an absolute value > 1 , and the equilibrium (\bar{x}, \bar{P}) can never be stable. Since $\det J$ is increasing in λ while $\text{tr } J$ is decreasing, and $(\text{tr } J, \det J)|_{\lambda=1} = (1, 1)$, we have complex eigenvalues for all $\lambda > 0$. This means that small deviations from the steady-state level in each case lead to diverging oscillations.

Even though the Nicholson Bailey model is quite simple, it can reflect the dynamic behaviour of such a system quite well. As an example, consider the data for *Encarsia formosa* (a wasp which acts as the parasitoid) and *Trialeurodes vaporariorum* (a whitefly which acts as parasitoid), observed in a laboratory experiment by Burnett [28]. The result is shown in Fig. 2.44. Remark that rounding and numerical approximations may have large effects in such systems! The behaviour can be checked by using a simple OCTAVE code, which can be found in the Appendix.

Since the Nicholson-Bailey model is unstable for all parameter values, but most natural host-parasitoid system are more stable, it probably makes sense to check modifications of the model. Let us introduce the following assumptions: If no parasitoids are there, the hosts population only grows to a limited density, corresponding to the carrying capacity of the environment. In the equations, this yields

$$\begin{aligned} x_{n+1} &= x_n \lambda(x_n) e^{-aP_n}, \\ P_{n+1} &= cx_n(1 - e^{-aP_n}), \end{aligned}$$

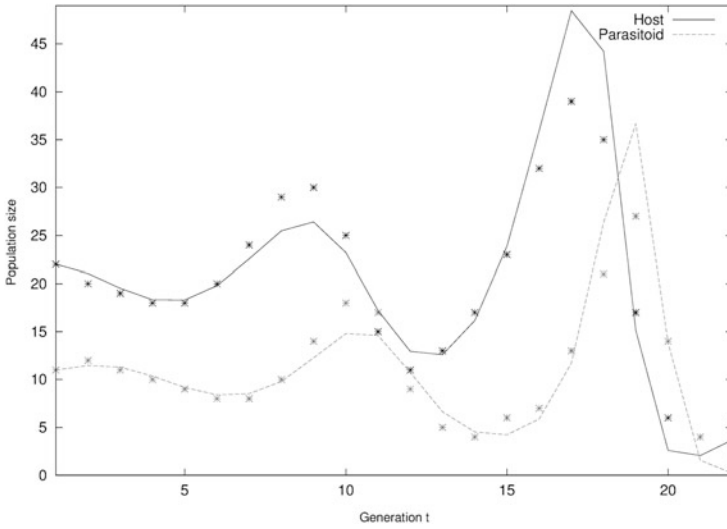


Fig. 2.44 Comparison of the laboratory experiment by Burnett [28] with the simulations of the Nicholson Bailey model, using the parameter values $c = 1$, $\lambda = 2$ and $a = 0.067$, and starting with the initial populations $x_0 = 22$ and $P_0 = 11$

where the growth rate is

$$\lambda(x_n) = e^{r(1-x_n/K)}.$$

In absence of the parasitoids, the host population grows up (or declines if $x_n > K$) until the capacity $x_n = K$. The revised model reads

$$x_{n+1} = x_n e^{r(1-x_n/K) - aP_n}$$

$$P_{n+1} = cx_n(1 - e^{-aP_n}).$$

This system is more complicated to discuss (e.g. it is not possible to get explicit expressions for the coexistence point (\bar{x}, \bar{P})), so we will not go into the details here, but Beddington et al. [19] have studied this model in detail and found that it is stable for a wide range of realistic parameter values.

2.3.2.11 Conclusions

We considered models for interacting populations. Such systems show in general richer dynamics and more complex behaviour as the linear models we looked at before. The interactions we focus here have a distinct structure: the prey has a positive effect on the predator (more prey leads to a higher growth rate of predators,), while predators have a negative effect on prey (more predators will decrease the

growth of prey). We show later in Chap. 5, Theorem 5.5, that this is an indication in compartmental models that stable periodic orbits exists (“stable periodic orbits” are defined there).

The main part of the section has been devoted to techniques that allow to detect or exclude periodic orbits: Lyapunov functions, the Theorem of Poincaré-Bendixson and the negative criterion of Bendixson-Dulac have been central tools.

The presence of oscillatory behaviour in ecological systems can be easily overlooked, as real world systems are always perturbed by extrinsic influences like weather or intrinsic stochasticity caused by small population sizes of some species. Oscillations can be – at least on the first glance – misinterpreted as fluctuations caused by perturbations. It is therefore of interest to be aware of situations where intrinsic oscillations may appear.

2.3.3 *Competition Models*

Competition yields a completely different structure than predator-prey models, as they are not hierarchic (in contrast to predator-prey models). If we visualise the species as nodes in graph, and draw a directed edge from the species which is eaten to the species which eats it (the arrows indicate the energy flow in the system), then the predator-prey system corresponds to a completely ordered graph, while a competing species are not ordered. Often this graph just described is used to introduce trophic levels: the root of such a graph are primary producers like plants and algae which utilise abiotic energy sources like sunlight or the chemical energy of black smokers in the deep see to sustain their life. The next trophic level are individuals that feed on these plants like rabbits or cows. Predators form the third level etc. In this sense, a predator-prey system consists of more trophic levels than a competition system: we may expect a less complex behaviour for competition. And indeed, periodic orbits do not play a major role, but we will almost always find that competition systems tend to stationary states. The central question for these systems is the persistence of all species: the main finding is the principle of competitive exclusion, which indicates that generically the number of persisting species cannot exceed the number of different resources available.

2.3.3.1 *The Chemostat*

The chemostat is a famous system which is often used in mathematical biology, ecology and biotechnology to investigate existing competitive systems or to produce biotechnological products. It is also called “Bio-reactor” or “Continuously stirred tank reactor (CSTR)” and is utilised as an instrument in laboratories, e.g. to study fermentation processes. As living organisms, we mention mainly bacteria, as they are typically used in the chemostat. The schematic working principle can be seen in Fig. 2.45. Substrate flows into the bioreactor at a constant rate. In order to keep

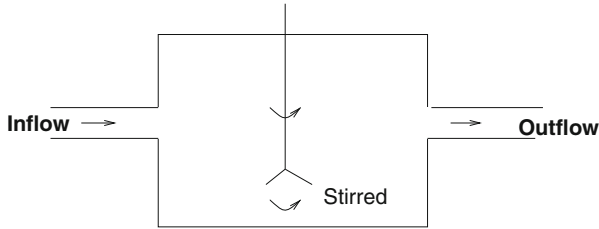


Fig. 2.45 The basic structure of the chemostat: By the inflow, the substrate is brought into the chemostat, the outflow (equal to the inflow) not only removes remaining substrate, but usually also the living species, at the same rate

the reaction volume constant, fluid is removed at the same rate. Therefore, bacteria, substrate and metabolic products are washed out at the same rate at which substrate is provided. The population dynamics within the reaction vessel is determined by two processes: the growth of bacteria due to nutrient utilisation, and wash-out of bacteria. A nice introduction into the mathematical theory of chemostats can be found in the book of Smith and Waltman [214].

2.3.3.2 One Bacterial Species and One Nutrient

Let us start off with the simplest case: one nutrient with concentration $S(t)$ at time t , and one bacterial species with population density $x(t)$. We do not take into account the spatial structure of the reaction vessel as we assume the system to be well stirred. The inflow- and outflow rate – also called dilution rate – is D , and the concentration of substrate in the inflow is S_0 . The uptake of nutrient per bacterium depends on the substrate concentration. It is described by a function $\tilde{f}(S)$. There are three natural assumptions:

- No nutrient uptake if there is no nutrient, $\tilde{f}(0) = 0$
- The more nutrient the higher is the uptake $\tilde{f}'(S) > 0$ for $S > 0$
- There is a maximal uptake rate per bacterium, $\lim_{S \rightarrow \infty} \tilde{f}(S) = \tilde{f}_\infty < \infty$.

A function often used in practice is the so-called Michaelis-Menten function (that originally has been derived in the context of enzyme kinetics, see Sect. 5.1.3),

$$\tilde{f}(S) = \frac{V_{\max} S}{S + K_m}.$$

Nutrient that has been consumed is converted into biomass. There is a proportionality factor ζ that tells us how much bacteria are newly produced if one unit of substrate is consumed. All in all, we find the model

$$\begin{aligned}\dot{S} &= D(S_0 - S) - \tilde{f}(S)x \\ \dot{x} &= -Dx + \zeta x \tilde{f}(S).\end{aligned}$$

Defining $s = \zeta S$, $s_0 = \zeta S_0$, $\zeta f(s) = \tilde{f}(s/\zeta)$ yields

$$\begin{aligned}\dot{s} &= D(s_0 - s) - f(s)x \\ \dot{x} &= -Dx + xf(s).\end{aligned}$$

We observe that $(s + x)' = Ds_0 - D(x + s)$ and hence $x + s = s_0 + Ce^{-Dt}$ where C is a constant that depends on the initial conditions. This equation has been made possible by the rescaling of S : instead of its natural units, we now measure the substrate concentration by biomass-equivalence units. Therefore,

$$x' = -Dx + f(s) = -Dx + xf(s_0 - x + Ce^{Dt}) = -Dx + xf(s_0 - x) + \mathcal{O}(e^{-Dt}).$$

We are allowed to apply the theorem about asymptotic autonomous systems. If we can show that the autonomous ODE $x' = -Dx + xf(s_0 - x)$ only possesses isolated stationary points (and no heteroclinic or homoclinic cycle), we know that the original model tends to a stationary point. As $x' = -Dx + xf(s_0 - x)$ is one-dimensional, all ω -limit sets are either empty or consist of stationary points. The stationary points of this equation are $x = 0$ or given by the solution of $f(s_0 - x) = D$. Re-inserting $s = s_0 - x$ again, and denoting the non-trivial stationary point by (x^*, s^*) , we find the decisive equation

$$f(s^*) = D.$$

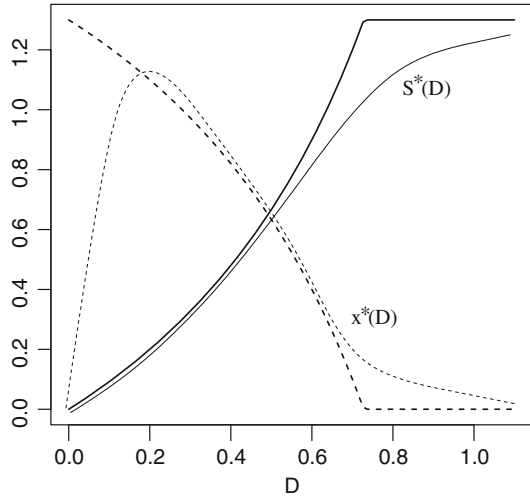
As $f(\cdot)$ is strictly increasing, this equation has at most one solution. If this solution is located in the interval $[0, s_0)$, we have found a non-trivial stationary point with population density $x^* = s_0 - s^*$. It is simple to see that the non-trivial stationary point is stable if it exists.

Result: If $f(s_0) > D$, there is a unique non-trivial stationary point $(x, s) = (x^*, s^*)$ with $x^* > 0$ given by $f(s^*) = D$ and $x^* = s_0 - s^*$. In this case, this stationary point is globally stable in $\{(x, s) \mid x > 0, s \geq 0\}$. If $f(s_0) \leq D$ only the trivial stationary state $(x, s) = (0, s_0)$ exists in the positive quadrant, and is globally stable.

We can understand this result in the following way: D acts as a death rate, $f(S)$ is a reproduction rate. In equilibrium, both rates have to balance, $D = f(S)$. The maximal reproduction rate possible is given at $s = s_0$. Thus, if $D \geq f(s_0)$ the population growth cannot balance the wash-out effect.

Consider D as an independent variable (indeed, D and s_0 are the only components that can be controlled relatively easily in an experiment) and consider s^* and x^* as functions depending on D . As $f(s^*) = D$, it is relatively simple to sample the function $f(s^*)$ experimentally: we only need to measure s^* for several values of D . The graph of $s^*(D)$ follows $f^{-1}(D)$ until it hits the level s_0 , where it stays for larger values of D . Similarly, $x^*(D)$ will decrease from s_0 (for $D = 0$) to zero (for $D = f(s_0)$) where it stays (see Fig. 2.46)

Fig. 2.46 Basic chemostat model with $f(s) = 1.2s/(s + 1.4)$ and $s_0 = 1.3$: stationary states over dilution rate D . *Solid lines* corresponds to substrate, *dashed lines* to population size. *Thick lines* denote model predictions, *thin lines* sketch the behaviour of experimental systems



If the dilution rate is neither very small nor very large, we find a nice agreement to typical observations; data like that can be e.g. found in [17]. We find disagreement for very small and very large dilution rates. For small dilution rates the model predicts an increasing population size, but the cell number breaks down; for large dilution rates we expect the wash-out effect to kill the population. What we find is a persistence on a low level. We need to take into account additional effects in order to obtain a more realistic model.

Maintenance energy: Cells have a certain need for energy in order to maintain a basic level of their metabolism. This means, part of the nutrient consumed is not converted into offspring. Let us assume that there is a rate m that describes the nutrient uptake for maintenance, we derive at the following variant of our chemostat-model

$$\begin{aligned}\dot{s} &= D(s_0 - s) - (m + f(s))x \\ \dot{x} &= -Dx + xf(s).\end{aligned}$$

We still go for stationary states; of course, we should first prove that the ω -limit sets are stationary states indeed, but we leave out this rather boring part. One equation for stationary states is still given by $D = f(s^*)$. This means, the s^* -component of the stationary states (in dependence on D) does not change. This is different for the x^* -component, as

$$x^* = \frac{D(s_0 - s^*)}{f(s^*) + m} = \frac{D(s_0 - s^*)}{D + m}.$$

Thus, if $m > 0$, $x^*(D) \rightarrow 0$ for $D \rightarrow 0$. For $D \gg m$, the term $D/(D + m) \approx 1$. This is, this effect will only change $x^*(D)$, and only for $D \ll 1$: The population breaks down for D small, as can be observed in experiments.

Attachment to the vessel wall: If D becomes large, we expect the wash-out effect to take over and to kill the population. Experiments show that the population may persist nevertheless. One reason can be that the assumption of a well stirred system is wrong: some bacteria may attach to the surface of the vessel and in this way avoid to be washed out. We assume a fixed subpopulation of size K_w attached to the vessel surface. The descendants of this population are assumed to be freely swimming (as, e.g., there is no space left where new bacteria may attach). The model equation read in this case

$$\begin{aligned}\dot{s} &= D(s_0 - s) - f(s)(K_w + x) \\ \dot{x} &= -Dx + (K_w + x)f(s).\end{aligned}$$

This variant is slightly more involving than the others, as the simple connection between D and $f(s^*)$ is lost. However, adding up the two equations shows that asymptotically still $x^* + s^* = s_0$ is valid. This observation allows to rewrite the equation $\dot{s} = 0$ in the following way:

$$f(s^*) = D \frac{s_0 - s^*}{K_w + s_0 - s^*} =: h(s^*).$$

While $f(\cdot)$ is increasing, $h(\cdot)$ is decreasing; moreover, for all $D > 0$ we find

$$f(0) = 0 < \frac{D s_0}{K_w + s_0} = h(0), \quad f(s_0) > 0 = h(s_0).$$

Therefore, for all $D > 0$ there is exactly one solution of $f(s^*) = h(s^*)$. As this solution is within the interval $[0, s_0]$ it corresponds to a non-trivial stationary state. Only asymptotically, for $D \rightarrow \infty$, we have $s^*(D) \rightarrow s_0$ and $x^*(D) \rightarrow 0$. This result is in line with the experimental observations.

2.3.3.3 Two Species and One Substrate: Competition Model

The chemostat allows to formulate one specific mechanism of competition in detail: the competition for nutrient. Of course, species also compete for other resources like space or light. However, the competition for nutrient is perhaps the most common and prototypical competition. Let us consider two species in the system denoted by x_1 and x_2 . Both follow a dynamics similar to that discussed before – given the nutrient density S , they will not interact at all, and we find in the simplest case [200]

$$\begin{aligned}\dot{S} &= D(S_0 - S) - \tilde{f}_1(S)x_1 - \tilde{f}_2(S)x_2 \\ \dot{x}_i &= -Dx_i + \zeta_i x_i \tilde{f}_i(S), \quad i = 1, 2.\end{aligned}$$

We rescale the units of x_i s.t. one unit of population i can be generated from one unit of substrate. This is, $y_i = x_i/\zeta_i$, and $f_i(S) = \zeta_i \tilde{f}_i(S)$. Then,

$$\begin{aligned}\dot{S} &= D(S_0 - S) - f_1(S)y_1 - f_2(S)y_2 \\ \dot{y}_i &= -Dy_i + y_i f_i(S), \quad i = 1, 2.\end{aligned}$$

For the functions $f_i(\cdot)$ we assume the same conditions as for $f(\cdot)$ in the last section: $f_i(0) = 0$, $f'_i(\cdot) > 0$, and $\lim_{S \rightarrow \infty} f_i(S) < \infty$. We will analyse, step by step, the long term behaviour of this model: first we exclude the periodic orbits, then we determine the stationary points, and last we investigate the stability of these stationary points.

Exclude periodic orbits

All trajectories starting in the positive octant are globally bounded (why?). In order to analyse the model, we wish to show that asymptotically, all trajectories tend to stationary points. If we sum up the three equations we derive at

$$\frac{d}{dt}(S + y_1 + y_2) = DS_0 - D(S + y_1 + y_2)$$

i.e., we know that

$$S(t) + y_1(t) + y_2(t) \rightarrow S_0$$

exponentially fast (the last fact, that the convergence is exponentially fast, is important!). We may now use the theorem about asymptotically autonomous ODEs. Thereto we consider the system

$$\begin{aligned}\dot{z}_1 &= -Dz_1 + z_1 f_1(S_0 - z_1 - z_2) \\ \dot{z}_2 &= -Dz_2 + z_2 f_2(S_0 - z_1 - z_2).\end{aligned}$$

This is a two-dimensional system. If we are able to exclude periodic orbits and homoclinic orbits/heteroclinic cycles, we are done: the theorem of Poincaré-Bendixson tells us that the solution tend to a stationary point, and thus the solution of our original system does so, and thus the principle of competitive exclusion holds true.

We apply the negative criterion of Bendixson, scaling the vector field by $1/(z_1 z_2)$:

$$\begin{aligned}& \frac{\partial}{\partial z_1} \left[\frac{1}{z_1 z_2} (-Dz_1 f_1(S_0 - z_1 - z_2)) \right] + \frac{\partial}{\partial z_2} \left[\frac{1}{z_1 z_2} (-Dz_2 f_2(S_0 - z_1 - z_2)) \right] \\ &= -\frac{1}{z_2} f'_1(S_0 - z_1 - z_2) - \frac{1}{z_1} f'_2(S_0 - z_1 - z_2) < 0.\end{aligned}$$

Hence the divergence of the vector field (scaled by $1/(z_1 z_2)$) is negative, and necessarily the solution tends to a stationary point. Hence, this is also true for the original, three dimensional, system.

Find stationary points

The linearity of the population dynamics yields exponential growth until the resource decreases at a level where mortality and growth rate balance or the corresponding population did vanish from the system: a stationary point satisfies (with $S = S_0 - z_1 - z_2$)

$$0 = -Dz_i + z_i f_i(S) = z_i (f_i(S) - D).$$

I.e., for a stationary point where species z_i is present, it follows that $f_i(S) = D$,

$$S = S_i^* \quad \text{with} \quad f_i(S_i^*) = D.$$

If there are positive solutions S_i^* of $f(S_i^*) = D$ that are smaller than S_0 , both species are able to survive in the absence of the other species; the corresponding population size is $z_i^* = S_0 - S^*$. However, generically, $S_1^* \neq S_2^*$, s.t. either species one or species two survives, but both species cannot coexist. Only at nongeneric points, where $S_1^* = S_2^*$ and $f_i(S_i^*) = D$, coexistence is possible: in this case, we find a line of stationary points, the set

$$\{(z_1, z_2) \mid S_0 - z_1 + z_2 = S_1^*\}$$

consists of stationary points only (see Fig. 2.47).

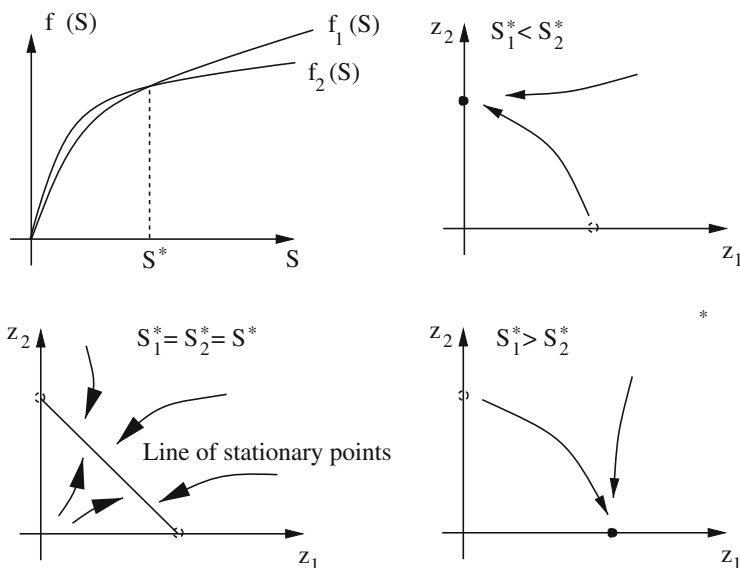


Fig. 2.47 Different cases for the two-species, one substrate chemostat model

Stability analysis of these stationary points

We consider the local stability of the single-species solutions in the two species model. We know from the analysis of a single species, that without a second species the persistence points is always stable. In order to decide about the stability properties, the only thing we need to know is if or if not the second species is able to invade the stationary persistence point of one species.

Claim $(z_1^*, 0, S_1^*)$ is linearly stable if $f_2(S_1^*) < f_1(S_1^*)$ and linearly unstable if $f_2(S_1^*) > f_1(S_1^*)$.
 $(0, z_2^*, S_2^*)$ is linearly stable if $f_1(S_2^*) < f_2(S_2^*)$ and linearly unstable if $f_1(S_2^*) > f_2(S_2^*)$.

Proof If we consider the stationary point $(y_1^*, 0, S_1^*)$, and linearise the equation for y_2 at this point,

$$z_1 = z_1^* + u_1, \quad y_2 = 0 + u_2$$

where u_1 and u_2 are small. Then,

$$\begin{aligned} u_2' &= (0 + u_2)' = z_2' = -Dy_2 + y_2 f_2(S_0 - z_1 - z_2) \\ &= -Du_2 + u_2(f_2(S_0 - z_1^* - u_1 - u_2)) \\ &= -Du_2 + u_2(f_2(S_0 - z_1^*) + \mathcal{O}(u_1) + \mathcal{O}(u_2)) \\ &= u_2[f_2(S_0 - z_1^*) - D] + \mathcal{O}(u_1 u_2) + \mathcal{O}(u_2^2) \\ &\approx u_2[f_2(S_0 - z_1^*) - D] = u_2[f_2(S_1^*) - D]. \end{aligned}$$

The stationary point $(z_1^*, 0, S_1^*)$ is locally stable, if

$$f_2(S_1^*) < D$$

and linear unstable for the reversed inequality. We know that in the single-species solution for species one present, $D = f_1(S^*)$. Hence, $(y_1^*, 0, S_1^*)$ is locally stable if

$$f_2(S_1^*) < f_1(S_1^*)$$

and unstable else. A symmetric result can be derived for the stationary state $(0, y_2^*, S_2^*)$, which is locally stable if $f_1(S_2^*) < f_2(S_2^*)$. \square

We are able to rewrite this stability result in terms that are more easy to interpret:

Claim $(z_1^*, 0, S_1^*)$ is linearly stable if $S_1^* < S_2^*$ and linearly unstable if $S_1^* > S_2^*$;
 $(0, z_2^*, S_2^*)$ is linear stable if $S_2^* < S_1^*$ and linear unstable if $S_2^* > S_1^*$;
 where, like before, $S_i^* = S_0 - y_i^*$.

Proof Let $S_1^* < S_2^*$. As $f_2(S_2^*) = D$ and $f_2'(\cdot) > 0$, we find (because of $S_1^* < S_2^*$) that $f_2(S_1^*) < D = f_1(S_1^*)$, i.e., $(y_1^*, 0, S_1^*)$ is linear stable.

Similarly, as $f_1(S_1^*) = D$ and $f_1'(\cdot) > 0$, we find because of $S_1^* < S_2^*$ that $f_1(S_2^*) > D = f_2(S_2^*)$, i.e., $(y_1^*, 0, S_1^*)$ is linear stable.

The stability result for $(0, y_2^*, S_2^*)$ follows by symmetry reasons. \square

One may interpret this result as follows: both species will grow and therewith decrease the substrate level until wash-out effect and growth balance. If $S_1^* < S_2^*$, the species one will decrease the nutrient concentration until S_1^* is reached. This level, however, is not sufficient for species two to survive: the growth rate $f_2(S_1^*)$ is smaller than the wash-out rate s.t. species two will go extinct, and only species one persists. This observation bears some similarity with the pessimisation principle that is one driving force of evolution; we will discuss this concept in Sect. 7.2.

If we draw f_1 and f_2 (see Fig. 2.47, left upper subfigure), we may determine which state is locally stable. For given D , the possible substrate density in the stationary states are solutions of $f_i(S) = D$, i.e., the intersection of the graphs with the line horizontal line $y = D$. The function f_i that crosses the line first has the lower equilibrium substrate concentration S_i^* and thus can out-compete the other population. Only at the bifurcation point, where the nongeneric condition

$$D = f_1(S_1^*) = f_2(S_2^*)$$

holds true, coexistence is possible: The line of stationary points “carries” the stability of one point to the other.

2.3.3.4 Excursion: Volterra’s Generic Competition Model

The two-species-one-substrate chemostat model describes a certain mechanism for competition between the two species. Volterra introduced a generic model for two interacting populations, assuming two basic properties:

- Two species compete for the same food (limited) – e.g. for a territory which corresponds to food resource
- Each species grows according to Verhulst and participates at the capacity of the other species.

These assumptions yield Volterra’s competition model,

$$\begin{aligned}\dot{x}_1 &= r_1 x_1 \left(1 - \frac{x_1 + b_1 x_2}{K_1} \right) \\ \dot{x}_2 &= r_2 x_2 \left(1 - \frac{x_2 + b_2 x_1}{K_2} \right).\end{aligned}$$

K_i denotes the capacity of species i ($i = 1, 2$), b_i indicates how much one species participates in the resources of the other species (it is also called the competitive effect), and r_i is the birth rate of species i . If two species are similar to each other, we find approximately $b_1 = b_2 = 1$.

It is sensible to simplify a model with so many parameters. This can again be done by rescaling. With

$$u_1 = \frac{x_1}{K_1}, \quad u_2 = \frac{x_2}{K_2}, \quad \tau = r_1 t, \quad \rho = \frac{r_1}{r_2}, \quad a_1 = b_1 \frac{K_2}{K_1}, \quad a_2 = b_2 \frac{K_1}{K_2},$$

we derive at

$$\begin{aligned} \frac{du_1}{d\tau} &= u_1(1 - u_1 - a_1 u_2) = f_1(u_1, u_2) \\ \frac{du_2}{d\tau} &= \rho u_2(1 - u_2 - a_2 u_1) = f_2(u_1, u_2) \end{aligned}$$

and the analysis is much easier!

Using the negative criterion of Bendixson and Dulac, it can easily be shown that no periodic orbits can exist in such a system:

The divergence of the vector field scaled by $\frac{1}{u_1 u_2}$ yields

$$\frac{\partial \left(\frac{1}{u_1 u_2} f_1(u_1, u_2) \right)}{\partial u_1} + \frac{\partial \left(\frac{1}{u_1 u_2} f_2(u_1, u_2) \right)}{\partial u_2} = -\frac{1}{u_2} - \frac{\rho}{u_1} < 0.$$

The isoclines lie on both coordinate axis and on two additional lines:

$$\begin{aligned} \dot{u}_1 = 0: \quad & u_1 = 0 \quad \text{or} \quad u_1 + a_1 u_2 = 1 \\ \dot{u}_2 = 0: \quad & u_2 = 0 \quad \text{or} \quad a_2 u_1 + u_2 = 1. \end{aligned}$$

Thus, there are four stationary points in general:

$$P_1 = (0, 0), \quad P_2 = (1, 0), \quad P_3 = (0, 1), \quad P_4 = (\bar{u}_1, \bar{u}_2),$$

where

$$\bar{u}_1 = \frac{a_1 - 1}{a_1 a_2 - 1}, \quad \bar{u}_2 = \frac{a_2 - 1}{a_1 a_2 - 1}.$$

Note that the coexistence point may be outside of the biological meaningful area, depending on the parameter values.

The general Jacobian reads

$$J(u_1, u_2) = \begin{pmatrix} 1 - 2u_1 - a_1 u_2 & -a_1 u_1 \\ -\rho a_2 u_2 & \rho(1 - 2u_2 - a_2 u_1) \end{pmatrix}.$$

For $a_1 = a_2 = 1$ these isoclines are parallel. But it is possible, to have parameters a_1 and a_2 which are lying nearby, but there is still no intersection point in the positive area. Let us first consider this case.

Case 1: $a_1 < 1$ and $1 < a_2$ The system exhibits three stationary points:

$$(0, 0), \quad (0, 1), \quad (1, 0).$$

The Jacobian matrices in these stationary points are:

- $J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & \rho \end{pmatrix} \leadsto (0, 0)$ is an unstable node
- $J(0, 1) = \begin{pmatrix} 1 - a_1 & 0 \\ -\rho a_2 & -\rho \end{pmatrix} \leadsto$ we have one positive eigenvalue $1 - a_1$ and one negative eigenvalue $-\rho$, which implies that $(0, 1)$ is a saddle point.
- $J(1, 0) = \begin{pmatrix} -1 & -a_1 \\ 0 & \rho(1 - a_2) \end{pmatrix} \leadsto$ both eigenvalues are negative, thus $(1, 0)$ is a stable node.

The two populations do not coexist, but u_2 is out-competed by u_1 . As we have the condition

$$a_1 = b_1 \frac{K_2}{K_1} < 1 < b_2 \frac{K_1}{K_2} = a_2$$

either the carrying capacity K_1 is larger than K_2 , or the competition effect b_1 is much weaker than b_2 .

Case 2: $a_1 > 1$ and $1 > a_2$ This case parallels case 1, only that u_1 and u_2 switch their roles.

Case 3: $a_1, a_2 < 1$ In this case, a coexistence point shows up, thus, there are four stationary points. The Jacobian matrices in these stationary points are:

- $J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & \rho \end{pmatrix} \leadsto (0, 0)$ stays to be an unstable node
- $J(0, 1) = \begin{pmatrix} 1 - a_1 & 0 \\ -\rho a_2 & -\rho \end{pmatrix} \leadsto$ we have a saddle point.
- $J(1, 0) = \begin{pmatrix} -1 & -a_1 \\ 0 & \rho(1 - a_2) \end{pmatrix} \leadsto$ also a saddle.
- $J(\bar{u}_1, \bar{u}_2) = \begin{pmatrix} 1 - 2(\frac{1-a_1}{1-a_1a_2}) - a_1(\frac{1-a_2}{1-a_1a_2}) & -a_1\frac{1-a_1}{1-a_1a_2} \\ -\rho a_2\frac{1-a_2}{1-a_1a_2} & \rho\left(1 - 2\frac{1-a_2}{1-a_1a_2} - a_2\frac{1-a_1}{1-a_1a_2}\right) \end{pmatrix}$
 $= \frac{1}{1-a_1a_2} \begin{pmatrix} -(1-a_1) & -a_1(1-a_1) \\ -\rho a_2(1-a_2) & -\rho(1-a_2) \end{pmatrix}$

We easily find $\text{tr}(J(\bar{u}_1, \bar{u}_2)) < 0$ and

$$\det(J(\bar{u}_1, \bar{u}_2)) = \frac{\rho(1-a_1)(1-a_2)}{1-a_1a_2} > 0.$$

The coexistence point is a stable node.

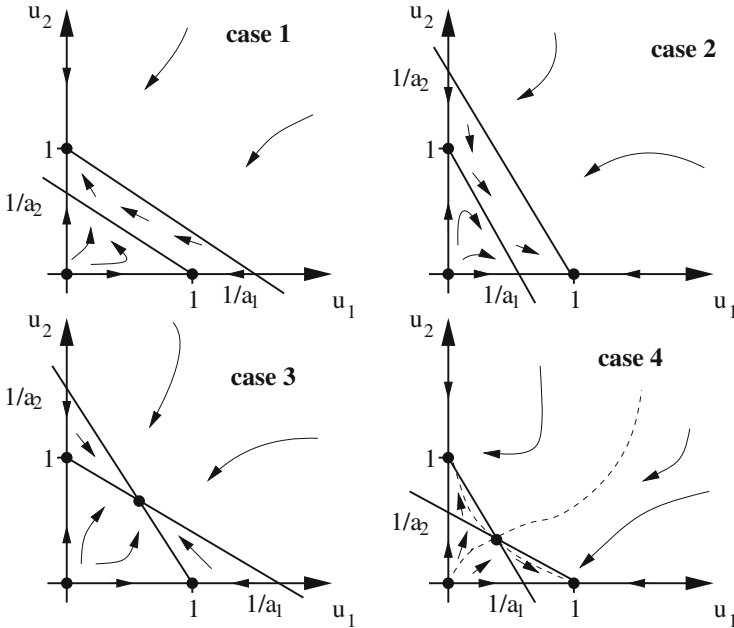


Fig. 2.48 The isoclines and qualitative behaviour of the solutions for the competition model. *Black bullets* denote stationary points, *straight lines* indicate isoclines, and the *arrows* sketch the flow of the vector field, the *dashed lines* in case 4 denote heteroclinic orbits. The four cases are discussed in the text

Case 4: $a_1, a_2 > 1$ Similar computations as in case 3 show that $(0, 0)$ and (\bar{u}_1, \bar{u}_2) are unstable, but $(1, 0)$ and $(0, 1)$ are stable nodes. In this case, we find a bistable behaviour (see Fig. 2.48): Depending on the initial condition either the first or the second species dies out; in any case they will not coexist.

In all cases but in case 3 the two species will not coexist. What is special in case three? The condition for this situation to occur reads

$$a_1 = b_1 \frac{K_2}{K_1} < 1, \quad b_2 \frac{K_1}{K_2} = a_2 < 1.$$

This is, b_1 as well as b_2 must not be too large: this setup describes two populations that mainly use different resources and compete only weakly. In any case where competition is substantial, only one species will survive. This behaviour is also called the “exclusion principle of Volterra”. One famous example for such a system was considered in [166]. More examples and information about this principle can be found e.g. in [58, 91, 180, 202].

2.3.3.5 General Chemostat Model

Of course, in general we do have more than two species and more than two resources in a system. The basic model for a chemostat with n species and m resources reads

$$\begin{aligned}\dot{S}_j &= D(S_j^0 - S_j) - \sum_{i=1}^n f_{i,j}(S_1, \dots, S_m)x_i, & j = 1, \dots, m \\ \dot{x}_i &= x_i \left(\sum_{j=1}^m f_{i,j}(S_1, \dots, S_m) - D \right), & i = 1, \dots, n.\end{aligned}\quad (2.16)$$

The functions $f_{i,j}(\cdot)$ represent the nutrient uptake of substrate j by species i . Note that the uptake of nutrient S_i in general depends on the presence of all other nutrients; it happens that bacteria feed preferentially on one nutrient and – in presence of this favourable nutrient – other substrates are ignored. It is straightforward to superimpose reasonable conditions on $f_i(\cdot)$, e.g.

$$f_{i,j}(S_1, \dots, S_m)|_{S_j=0} = 0, \quad \frac{\partial f_{i,j}(\cdot)}{\partial S_j} > 0, \quad f_{i,j}(\cdot) < f_{i,j}^\infty \in \mathbb{R}.$$

If we aim at equilibria where all species are present, we first of all find a set of nonlinear equations

$$\sum_{j=1}^m f_{i,j}(S_1, \dots, S_m) = D, \quad i = 1, \dots, n.$$

Generically, this equation possesses nontrivial solutions only for $n \leq m$. Of course, it is simple to construct examples for $n \leq m$ where we do find nontrivial solutions (let $f_{i,j}(S_1, \dots, S_m) = \delta_{i,j} \tilde{f}_i(S_i)$, i.e., let species i only feed on substrate i , which leads to the trivial case of n independent species). All in all, we expect for $n > m$ no equilibrium to exist where all species are present, and – if the $f_{i,j}$ are chosen appropriately – for $n \leq m$ all species may persist. This observation leads to the general principle of exclusion.

Principle of exclusion: If an ecosystem is based on m different resources, at most m different species competing for these resources can be sustained.

The first idea of a competitive exclusion principle was claimed already in 1934 by the Russian biologist Gause [81] (for two species with similar ecology). In 1960, this first statement was stated more precisely by Hardin and called “competitive exclusion principle” (CEP). It was stated that “ecological differentiation is the necessary condition for coexistence”. A later generalisation came to the result stated above, that n species cannot coexist on fewer than n resources.

In nature, there are some counterexamples, e.g. the biodiversity of many organisms. A famous example, “the paradox of the plankton”, can be found in

Hutchinson [131]. Indeed, there is a discrepancy between theoretical approach and experimental observation. A lot of examinations were done, from biological and from modelling view. Some advisement about coexistence in competition models can be found in [152].

2.3.3.6 Conclusion

In this section we proceeded with the investigation of interacting populations, this is, of nonlinear ODE models. We find the typical approach in the analysis of an ODE: first, determine the stationary points, then use Hartman-Grobman in order to obtain some information about their stability and the dynamics of the system near by. Search for bifurcations, in particular Hopf bifurcations (as transcritical and saddle-node bifurcation can be already detected from the stationary points). Try to prove or disprove the existence of periodic orbits. In two dimensions, Poincaré-Bendixson and the negative criterion of Bendixson are helpful.

In the case of competition models, we found that periodic orbits do not play a major role, but the trajectories tend to stationary points. This observation has a theoretical underpinning, that we discuss in Chap. 5, Theorem 5.10: due to the competition, each species has a negative effect on all other species in the system. In this case, one can show that stable periodic orbits will not appear. In the chemostat model, substrate has of course a positive influence on the species living in the system; however the theorem also covers this case.

The mathematical concept for competing systems leads to the principle of competitive exclusions, for sure one of the most important findings in this section. Often enough, this paradigm is also observable in nature. However, we will find below that intraguild predation (predation of a prey, consuming at the same time directly also the food of the prey) stabilises the system. Moreover, an ecosystem hasn't formed as it is, but one species after the other tried to invade. Some have not been successful, others did outcompete resident species. An ecosystem that we observe in nature has evolved a long time, and therefore it consists of many species that fit to each other (for a theory in this direction see [158]). This stochastic process favoured stable compositions and led to the relatively robust ecosystems we observe today.

2.3.4 Modelling Symbiosis

There are different definitions of symbiosis; the most general describes this term as persistent biological interaction between different species. We use it in the sense of mutualism, i.e., the interaction of (two) species, which helps the other (and vice versa). There are many different types of mutualism in nature, we only mention a few typical ones: Animals may eat (or bury) fruits and nuts and by that carry the seeds to other places (called seed-dispersal mutualism); microbes predigest food

for the host which is indigestible for the host otherwise and the host provides a protected, partially nutrient-rich environment (called digestive mutualism); or the well-known Clown fishes protect “their” sea anemones against predators, and the anemones vice versa provide a protected area e.g. for nesting for the Clown fishes (called protection mutualism).

For the modelling approach, it is also important to check how many species are involved and if the considered interaction is essential or only helpful. A basic model, with logistic growth for each population x_1 and x_2 and the assumption that mutualism ameliorates intraspecific competition (i.e., competition between the individuals of one species), reads

$$\begin{aligned}\dot{x}_1 &= r_1 x_1 \left(1 - \frac{x_1 - b_1 x_2}{K_1} \right) \\ \dot{x}_2 &= r_2 x_2 \left(1 - \frac{x_2 - b_2 x_1}{K_2} \right),\end{aligned}$$

similar to the competition model of Volterra. K_i denotes the capacity of species i , b_i is called the symbiosis effect, i.e., gives information about how strong the other species “helps” and increases the capacity of species i , r_i birth rate of species i . The analysis of this model can be done analogously to that of Volterra’s competition model and is left to the reader. Main problem appears: There may be unlimited growth, so for preventing this undesired possibility, modifications of the model are needed, see e.g. [152] for examples.

2.3.5 Food Chains and Food Webs with Three Trophic Levels

Let us first consider the most simplest food chain with three species. The lowest trophic level is denoted by R (resources), the second level by N (intermediate consumer) and the highest level by P (a predator). As we consider a food chain, the model reads

$$\begin{aligned}\dot{R} &= R[r(1 - R/K) - aN] \\ \dot{N} &= N(abR - \mu_1 - \alpha P) \\ \dot{P} &= P(\alpha\beta N - \mu_2).\end{aligned}$$

This means: The lowest level has a logistic growth, while the second level feeds on the first one and the third level feeds on the second one. We especially pay attention to the effect of a change in the carrying capacity K .

We always have the fixed point

$$(R_0, N_0, P_0) = (K, 0, 0).$$

This fixed point can be invaded by P if

$$abK - \mu_1 > 0 \quad \Leftrightarrow \quad K > K_1^* = \mu_1/(ab).$$

In this case, we find the fixed point

$$(R_1, N_1, P_1) = (\mu_1/(ab), r(1 - \mu_1/(abK))/a, 0).$$

Similarly to Rosenzweig's paradox of enrichment, the increase in the carrying capacity leads to an increase of P and not of R , i.e., the resources immediately go to the second trophic level.

Now we ask, if the species of the third trophic level is able to invade:

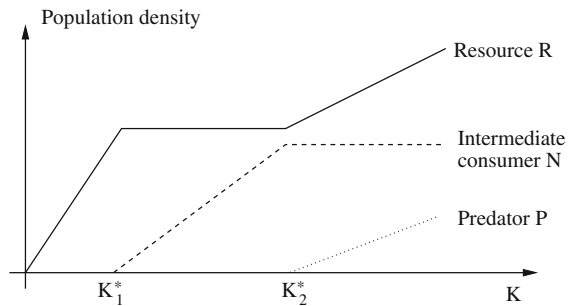
$$\begin{aligned} \alpha\beta N > \mu_2 &\quad \Leftrightarrow \quad \alpha\beta(1 - \mu_1/(abK))(r/a) > \mu_2 \\ \Leftrightarrow \quad K > K_2^* &= \frac{r\alpha\beta\mu_1}{(r\alpha\beta - a\mu_2)ab} = \frac{r\alpha\beta}{(r\alpha\beta - a\mu_2)} K_1^*. \end{aligned}$$

As the expression $(r\alpha\beta)/(r\alpha\beta - a\mu_2)$ is always > 1 if positive, we find in this case $K_2^* > K_1^*$ (the intermediate consumer needs to be established before the prey is able to invade). In the following, let us assume the positivity of K_1^* . If $K > K_2^*$, the predator P is only able to invade later giving raise to the fixed point

$$(R_2, N_2, P_2) = \left(K \left(1 - \frac{a\mu_2}{r\alpha\beta} \right), \frac{\mu_2}{\alpha\beta}, [abK \left(1 - \frac{a\mu_2}{r\alpha\beta} \right) - \mu_1]/\alpha \right).$$

As the intermediate level is now controlled by the top level, the lowest level is now able to participate from the increase of its carrying capacity. The energy flow upward is thus less efficient. However, in this case only the lowest and the top level gain by an increased carrying capacity (see the scheme in Fig. 2.49). Experimental laboratory experiments are able to confirm this theoretical prediction [140].

Fig. 2.49 Dependency of population structure in a food chain with three trophic levels on the carrying capacity of the resource



2.3.5.1 Food Webs with Three Trophic Levels

A food web is not linearly ordered like a chain. The simplest food webs with three trophic levels are presented in Fig. 2.50. Web (A) is a food chain, (B) represents the simplest type that is no chain any more; this web includes horizontal heterogeneity, (C) incorporates vertical heterogeneity (omnivory) and (D) exhibits both, horizontal as well as vertical heterogeneity.

Let us consider case (B); this is the direct generalisation of the food chain we analysed above. If the “bypass” (P feeds on R) is not too strong, the results will not change. However, the behaviour may be different if the predator is able to feed strongly not only on the intermediate consumer P but also on the resource R. At least we may expect (for appropriate parameter values) an additional fixed point with $N = 0$ but $R > 0$, $P > 0$.

The food web of case (B) can be formulated in a system of Lotka-Volterra type as follows

$$\begin{aligned}\dot{R} &= R[r(1 - R/K) - aN - a'P] \\ \dot{N} &= N[abR - \alpha P - \mu_1] \\ \dot{P} &= P[a'b'R + \alpha\beta N - \mu_2].\end{aligned}$$

We concentrate on stationary points and do not consider stability; this is a common approach in this field. However, as we have seen e.g. in the classical competition model coexistence points may be unstable and only indicate the location of a manifold that separated the regions where one resp. the other species goes extinct. Thus, the mere existence of a coexistence point indicates by no means that the species can coexist, indeed. So the results derived in this way should be treated with

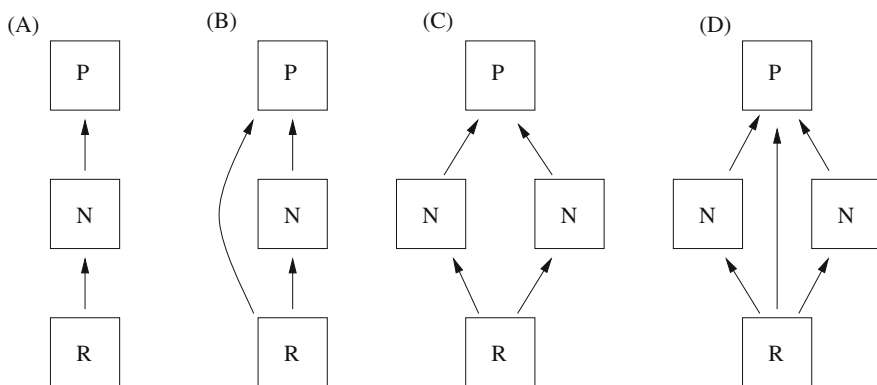


Fig. 2.50 Topology of simple food webs with three trophic levels. An arrow points from prey to predator, indicating the energy flow

cautions. We expect four stationary points, and three of them are already known to us (from the food chain).

(1) Resource only:

$$(R_0, N_0, P_0) = (K, 0, 0).$$

(2) Resource and intermediate consumer only:

$$(R_1, N_1, P_1) = (\mu_1/(ab), r(1 - \mu_1/(abK))/a, 0).$$

This point is feasible if

$$abK - \mu_1 > 0 \quad \Leftrightarrow \quad K > K_1^* = \mu_1/(ab).$$

(3) Resource and predator only:

$$(R_3, N_3, P_3) = (\mu_2/(a'b'), 0, r(1 - \mu_2/(a'b'K))/a').$$

This point is feasible if

$$a'b'K - \mu_2 > 0 \quad \Leftrightarrow \quad K > K_2^* = \mu_2/(a'b').$$

(4) All species present: In order to derive this stationary point $(R, N, P) = (R_4, N_4, P_4)$ let us assume that R_4 is already known to us. Then,

$$N_4 = \frac{\mu_2 - a'b'R_4}{\alpha\beta}$$

$$P_4 = \frac{abR_4 - \mu_1}{\alpha}.$$

We plug these equations into $\dot{R} = 0$ and find

$$0 = r - \frac{r}{K}R_4 - a \frac{\mu_2 - a'b'R_4}{\alpha\beta} - a' \frac{abR_4 - \mu_1}{\alpha}$$

$$\Rightarrow R_4 = K \frac{r\alpha\beta + a'\beta\mu_1 - a\mu_2}{r\alpha\beta + Kaa'(\beta b - b')}.$$

In order to find a positive solution, we need to check that (with this value of R_4) also N_4 and P_4 are positive. For that purpose, the inequalities

$$\frac{\mu_2}{a'b'} > K \frac{r\alpha\beta + a'\beta\mu_1 - a\mu_2}{r\alpha\beta + Kaa'(\beta b - b')} > \frac{\mu_1}{ab} \quad (2.17)$$

have to be checked. We especially pay attention to the dependence of the coexistence point on K (the energy that is available to the complete system) and a' (the strength of omnivory, i.e., the link from predator to resource). We find immediately that the two species cannot coexist if the intraguild predation is too heavy, i.e., if

$$\frac{\mu_2}{a'b'} > \frac{\mu_1}{ab} \Leftrightarrow a' > a'_* = a \frac{\mu_2 b}{\mu_1 b'}.$$

Let $K_{3,a'}^*$ denote the value of the carrying capacity that satisfies the first inequality of (2.17) with “ $=$ ”, and $K_{3,b'}^*$ that value of the carrying capacity, for which the second inequality becomes an equality. Hence,

$$\begin{aligned} \frac{\mu_2}{a'b'} &= K_{3,a}^* \frac{r\alpha\beta + a'\beta\mu_1 - a\mu_2}{r\alpha\beta + K_{3,a}^*aa'(\beta b - b')} \\ \Rightarrow \frac{r\alpha\beta\mu_2}{a'b'} + K_{3,a}^* \left(\beta\mu_2a\frac{b}{b'} - \mu_2a \right) &= K_{3,a}^* (r\alpha\beta + a'\beta\mu_1 - a\mu_2) \\ \Rightarrow K_{3,a}^* &= \frac{A_a}{a'(B_a + a'C_a)} \end{aligned}$$

where

$$\begin{aligned} A_a &= \frac{r\alpha\beta\mu_2}{b'} \\ B_a &= r\alpha\beta - \beta\mu_2a\frac{b}{b'} = \frac{\beta}{b'} (r\alpha b' - \mu_2ab) \\ C_a &= \beta\mu_1 \end{aligned}$$

From that, it follows that $A_a, C_a > 0$, while B_a may be larger as well as smaller than zero.

Now we determine in a similar way $K_{3,b}^*$,

$$K_{3,b}^* \frac{r\alpha\beta + a'\beta\mu_1 - a\mu_2}{r\alpha\beta + K_{3,b}^*aa'(\beta b - b')} = \frac{\mu_1}{ab}.$$

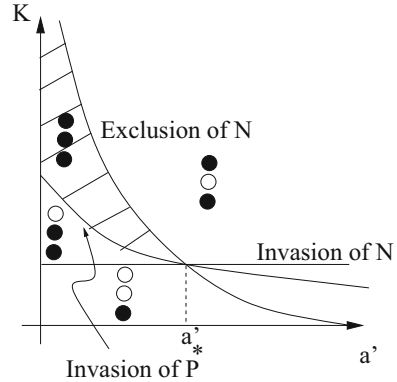
The structure of this expression is quite similar to that for $K_{3,a}^*$. The main difference is, that on the right hand side no a' appears. We find that

$$K_{3,b}^* (r\alpha\beta + a'\beta\mu_1 - a\mu_2) = \frac{\mu_1 r\alpha\beta}{ab} + K_{3,b}^* a \frac{\mu_1 a'(\beta b - b')}{ab}$$

and thus

$$K_{3,b}^* = \frac{A_b}{B_b + a'C_b}$$

Fig. 2.51 Population structure (all possible species present) for the omnivory model. The hatched region indicates the parameter set where coexistence of the predator and the intermediate consumer is possible



where

$$A_b = \frac{\mu_1 r \alpha \beta}{ab} > 0$$

$$B_b = a\mu_2 - r\alpha\beta$$

$$C_b = \beta\mu_1 - \mu_1(\beta b - b')/b = \mu_1 b'/b > 0$$

Let us assume that $B_a, B_b > 0$. In this case, we have three possibilities of the behaviour of the system if we increase K from very small to very large values (see Fig. 2.51):

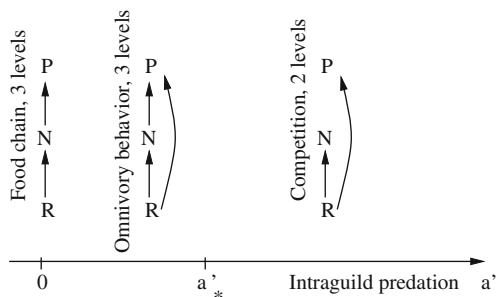
- (a) ($a' = 0$) resource present \rightarrow invasion intermed. consum. \rightarrow invasion predator
- (b) ($0 < a' < a'_*$) resource present \rightarrow invasion intermed. consum. \rightarrow invasion predator \rightarrow exclusion intermed. consum.
- (c) ($a'_* < a'$) resource present \rightarrow invasion intermed. consum.

or, alternatively,

resource present \rightarrow invasion predator

The system moves, depending on the strength of interguild predation a' , from the food chain with three levels to the competition model with one resource and two consumers (i.e., the third trophic level acts basically as a second species on the second trophic level). In between there is a transition zone: up to a certain value of K , the system looks like a food chain and allows for persistence of all three trophic levels. However, if K exceeds a certain value, the third trophic level basically feeds directly on the second trophic level and excludes the intermediate consumer. We move with a' from a food chain to competitive exclusion, i.e., effectively only two trophic levels (see Fig. 2.52).

Fig. 2.52 Intraguild predation moves the effective food web from the food chain to competitive exclusion



2.3.6 Exercises

Exercise 2.8 The following competition model was introduced by J.R. Buchanan, Lavery, Wagner, Wallace (Millersville University), Perry (Illinois State University), 2005 and describes competition among crayfish species subject to predation.

The interaction between two different species of crayfish is considered. Let u the invasive species, v the native species, then the model reads as follows:

$$\begin{aligned} u_{t+1} &= u_t e^{r_u(1-(u_t+c_v v_t)/K_u)} \\ v_{t+1} &= v_t e^{r_v(1-(c_u u_t+v_t)/K_v)}. \end{aligned}$$

All parameters are ≥ 0 and have the following meaning:

r_u : reproductive rate of the invasive species u

r_v : reproductive rate of the native species v

c_u : competitive effect of the native species on the invasive species

c_v : competitive effect of the invasive species on the native species

K_u : environmental carrying capacity for the invasive species

K_v : environmental carrying capacity for the native species

Can you interpret the equations – why do they describe competition?

Which is the condition for the existence of a coexistence point (i.e., a fixed point with $\bar{u} \neq 0$, $\bar{v} \neq 0$)? Please determine the coordinates of the coexistence point!

Which condition guarantees that the coexistence point is asymptotically stable?

(Hints: Use the fixed point condition for simplifying the general Jacobian matrix before you insert the coordinates of the coexistence point. Additionally: Since the formulae may grow up, it might help to use some short notations in between, e.g. $a = \frac{r_u}{K_u} \bar{u}$, $b = \frac{r_v}{K_v} \bar{v}$, $c = c_u c_v$).

Exercise 2.9 Here, we consider two species x_1 and x_2 which live together symbiotically. A simplified (nondimensionalised) version of the basic model reads:

$$\begin{aligned}\dot{x}_1 &= x_1(1 - x_1) + b_1x_1x_2 \\ \dot{x}_2 &= ax_2(1 - u_2) + b_2x_1x_2,\end{aligned}$$

where the constants a, b_1, b_2 are positive.

- How can the terms in this model be interpreted ?
- Please determine the stationary solutions of this model. Under which conditions for the coefficients a, b_1, b_2 is there a coexistence point in the biologically relevant domain?
- Please draw the isoclines and the slope field of the model (distinguishing the two cases $b_1b_2/a > 1$ and $b_1b_2/a < 1$)
- Please discuss the qualitative behaviour of this symbiosis system.

Exercise 2.10 The following special case of a two-species interaction model is given:

$$\begin{aligned}\dot{x} &= -\alpha x + \beta xy \\ \dot{y} &= -\gamma y + \delta xy\end{aligned}$$

- How can this model be interpreted from a biological point of view? (We assume all constants to be positive)
- Please analyse the behaviour of that model, concerning stationary points and their type, and draw the slope field, including a sketch for the solution curves.
- How can that behaviour be interpreted from a biological point of view?

Exercise 2.11 The system of May and Leonard was developed in 1975 in order to show that competitive interaction of three or more species can lead to an unexpected dynamical behaviour:

$$\begin{aligned}\dot{x}_1 &= x_1(1 - x_1 - \alpha x_2 - \beta x_3) \\ \dot{x}_2 &= x_2(1 - x_2 - \alpha x_3 - \beta x_1) \\ \dot{x}_3 &= x_3(1 - x_3 - \alpha x_1 - \beta x_2),\end{aligned}$$

where x_i denotes the population density of species i . The system is considered in the cone

$$C = \{x = (x_1, x_2, x_3) : x_i \geq 0, i = 1, 2, 3\}$$

Can you explain why it makes sense to call this system a competitive model?

Is there any connection to Volterra's competition model?

Please check the system for stationary points. Which types of coexistence are possible, depending on the parameters α and β ?

Exercise 2.12 We consider an oceanic ecosystem (following [27]), consisting of phytoplankton P feeding on (limited) nitrogen N and zooplankton Z feeding on the phytoplankton. The system is closed w.r.t. energy (nitrogen), i.e., nothing can appear or disappear. A simple model approach reads

$$\begin{aligned}\dot{N} &= aP + bZ - cNP \\ \dot{P} &= cNP - dPZ - aP \\ \dot{Z} &= dPZ - bZ\end{aligned}$$

Note that P and Z are taken to be in unit of mass of nitrogen which is incorporated in the plankton (to simplify the equations slightly).

- Please show that the mass of nitrogen is conserved by the system.
- Which stationary states are possible?
- How does the qualitative behaviour of the system depend on the parameter c ?

Exercise 2.13 The population dynamics of spruce budworms, which can defoliate the balsam fir, is described by the following model (in a non-dimensionalised form):

$$\dot{x} = rx \left(1 - \frac{x}{K}\right) - \frac{x^2}{1+x^2} =: f(x)$$

x denotes the population size, r is the growth rate and K the carrying capacity. (For the analysis, we fix the capacity to $K = 6$.)

- Which kind of interaction could be described by the second term $-\frac{x^2}{1+x^2}$?
- Fix K (e.g. $K = 6$), then we can use r as a bifurcation parameter. Please determine (at least) approximate values (exemplarily) for r , where the system has two/three/four stationary states. (Hint: Plot the graph of $f(x)$ – can be also done by a computer program; the range around $r \approx 0.61$ could be interesting)
- Which kind of bifurcation happens here?
- How can we interpret the result from a biological point of view?

Exercise 2.14 By photosynthesis, plants can take up carbon and incorporate it into their biomass. Let the biomass of plants be denoted by P and the biomass of herbivores by H . The herbivores are feeding on these plants. The following model

equations are given:

$$\begin{aligned}\dot{P} &= \phi - aP - bPH \\ \dot{H} &= ebPH - cH.\end{aligned}$$

- Please give a biological interpretation of these equations.
- Where are the stationary states of that system, and are they stable or not?
- What is the effect of increasing primary production ϕ ?
- Please sketch the possible phase planes for the system.

Exercise 2.15 In a chemostat two bacterial species are in competition for the same resources. We can model this situation as follows:

$$\begin{aligned}\dot{x}_1(t) &= x_1 \left(\frac{g_1 S(t)}{k_1 + S(t)} - m_1 \right) \\ \dot{x}_2(t) &= x_2 \left(\frac{g_2 S(t)}{k_2 + S(t)} - m_2 \right) \\ \dot{S}(t) &= D(S_0 - S(t)) - z_1 x_1 \frac{g_1 S(t)}{k_1 + S(t)} - z_2 x_2 \frac{g_2 S(t)}{k_2 + S(t)}.\end{aligned}$$

- Please explain the meaning of the parameters present in this model. Which assumptions are necessary on m_1, m_2 ?
- Define $f_i(S) := \frac{g_i S(t)}{k_i + S(t)}$, $y_i := z_i x_i$ and rescale the model (from now on, we will work with the system (y_1, y_2, S)).
- Usually, it is comfortable to reduce the dimension of the system. Which assumptions would you make, in order to reduce the system (y_1, y_2, S) to a 2D system?
- Does the 2D-model show periodic orbits?

Exercise 2.16 (difficult) Consider the chemostat with one species and periodic dilution rate,

$$\begin{aligned}y' &= -D(t)y + yf(S) \\ S' &= D(t)(S_0 - S) - yf(S)\end{aligned}$$

Assume that $f(x) \in C^2$, $f(0) = 0$, $f'(x) > 0$, $f''(x) < 0$ for $x \in \mathbb{R}_+$, $\lim_{x \rightarrow \infty} f(x) = f_\infty < \infty$, $D(t) \in C^0$, $D(t) > 0$, and $D(t+T) = D(t)$ for a given $T > 0$. Consider a non-negative, T -periodic solution $\hat{y}(t), \hat{S}(t)$. Define the average of a T -periodic

function $g(t)$ by

$$\langle g(t) \rangle = \frac{1}{T} \int_0^T g(t) dt.$$

(a) Show for the average yield $\langle D(t)y(t) \rangle$ that

$$\langle D(t)\hat{y}(t) \rangle = \langle \hat{y}(t)f(S_0 - \hat{y}(t)) \rangle.$$

(b) Let $h(x) = xf(S_0 - x)$, and compute $h''(x)$. Show that for a given periodic rate $D(t)$ there is some constant dilution rate d that leads to the same average yield.

(c) Let d^* be the constant dilution rate that gives the maximal yield d^*y (where y denotes the steady state population). Is d^* unique? Is there a periodic dilution rate that gives the same yield?

Exercise 2.17 In the paper of Jannasch et al. [136] an experiment with a chemostat is described. They work with the bacterium *Shewanella* sp.; in this experiment, two different dilution rates D and two different substrate concentrations S_0 (yeast extract) are used, and the steady state cell concentration x is measured.

D	S_0	x
0.066/h	10 mg/l	$2.2 \cdot 10^6$ cells/l
0.044/h	10 mg/l	$2.2 \cdot 10^4$ cells/l
0.066/h	1 mg/l	$0.9 \cdot 10^6$ cells/l
0.044/h	1 mg/l	$0.8 \cdot 10^5$ cells/l

Consider the simple chemostat model

$$x' = -Dx + \alpha xS$$

$$S' = D(S_0 - S) - \beta xS$$

Can you estimate the parameters of this model from the data?

Exercise 2.18 Consider a simple (Lotka-Volterra-type) predator-prey model describing a pest and its predator. In agriculture pesticides are used to fight the pest. Set up a model for the effect of pesticides, and determine the average level of predator and prey (pest). How is the pest population affected by the intensity of pesticide usage?

Appendix: Mathematical Ecology

1 Program Codes for the Mathematical Ecology Chapter

1.1 Exponential Growth

The following `simbTUM` code includes the standard (continuous) exponential growth model and compares/fits it to experimental data of *Pseudomonas putida*.

```
# Exponential growth of a bacterial population
\begin model expgrowth

# Setting state space
\begin states
# name; scale; init_val;
X; U; 336000*U;
time; 0.1*h; 0*h;
\end states
# Unit U corresponds here to number of cells per ml.

# Defining constants
\begin constants
    b := 0.68438/h; # growth rate
\end constants

# The ODE for exponential growth
\begin addTerm
    X' += b*X;
\end addTerm

\color blue

# Setting the data
\begin dataset pseudomonasputida
\begin style
    shape = box;
    color = red;
\end style
#\begin fit
#     computeError=true;
#     leastSquare=true;
#\end fit

time [h] X[U]
0  336000
2  500000
3  800000
4  1460000
5  6000000
6  18900000
```



```

7  40000000
8  81000000
9  100000000

\end dataset

\begin numeric
    timeHorizont=9*h;
\end numeric

\end model

```

1.2 Cobwebbing

The following OCTAVE code can produce nice cobwebbing graphs. The example uses $f(x) = rx(1 - x)$, i.e., the difference equation $x_{n+1} = rx_n(1 - x_n)$ which corresponds to the discrete logistic equation.

The first figure consists of four subfigures, to visualise the proceeding of the time steps better. The second figure shows the “jump size” between two iteration steps.

```

% First define the function f to be used.

function y=parabola(x,r)
    %Generates the function for the cobwebbing
    %Setting parameters
    % r=1.8;
    r=2.9;
    %Setting function
    y=r*x*(1-x);
endfunction

% This auxiliary function helps to get a nice graph
function bool=factoraux(steps, i, factor)
    bool=false;
    q=steps/factor;
    for j=1:factor
        p=q*j;
        if i==p
            bool=true;
        endif
    endfor
endfunction

```



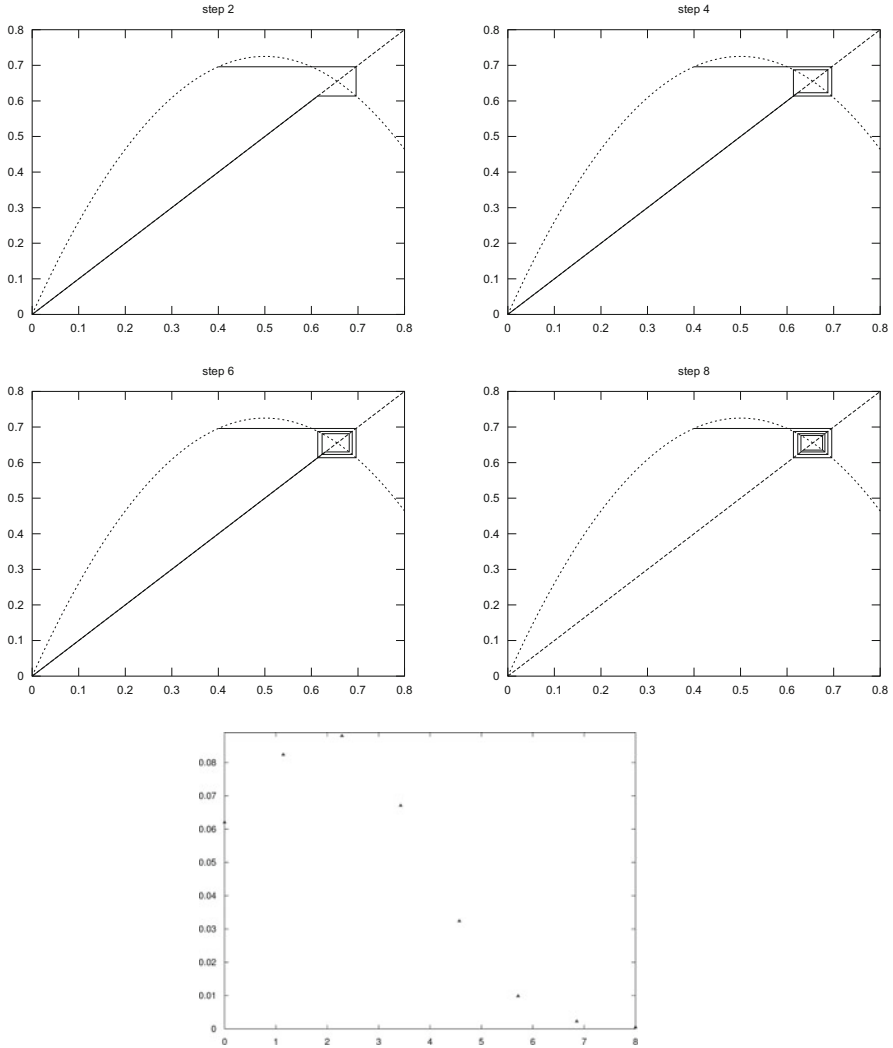
```
td=linspace(0,8,8);
```

```
figure
plot(td, d, '^')
```

%Alternatively: plotting just the final plot as a single figure:

```
figure
y=parabola(x);
%Setting Matrix Y
Y(1,2*steps-1)=x;
Y(2,2*steps-1)=y;
Y(1,2*steps)=y;
Y(2,2*steps)=y;
x=y;
%Getting Rows of Matrix Y for Plotting
A=Y(1,:);
B=Y(2,:);
% plot(A,B,T,g,T,f)
% black and white plot
plot(A,B,'k',T,g,'k',T,f,'k')
% Save the figure with colours
%print("cobwebbing_result.eps", "-color", "-deps")
% Save the figure without colours
print("cobwebbing_result.eps", "-deps")
```

The resulting figures are



1.3 Nicholson-Bailey

The following OCTAVE code represents the simulation of the discrete Nicholson-Bailey model (for a host-parasitoid system) and compares the model results with experimental findings from [28]. The model was introduced in Sect. 2.3.2.10.

```
% Nicholson-Bailey model
%
% x0: initial population size of the host
% P0: initial population size of the parasitoid
```

```

% lambda: host reproduction number
% c: average number of viable eggs per parasitoid on a single host
% a: searching efficiency of the parasitoid
% Nmax: maximum number of iterations

x0 = 22;
P0 = 11;
lambda = 2;
c = 1;
a = 0.067;
Nmax = 22;

x=zeros(Nmax,1);
P=zeros(Nmax,1);

x(1)=x0;
P(1)=P0;

for n=1:(Nmax-1)
    x(n+1) = lambda.*x(n).*exp(-a.*P(n));
    P(n+1) = c.*x(n).*(1-exp(-a.*P(n)));
end

lx= length(x);
M = 1:1:lx;
plot(M,x,'k',M,P,'r');
legend('Host','Parasitoid');
xlabel('Generation t');
ylabel('Population size');

hold on;

% values from the experiment of Burnett
x_exp = [22,20,19,18,18,20,24,29,30,25,15,11,13,17,23,32,39,35,17,6,4,6];
P_exp = [11,12,11,10,9,8,8,10,14,18,17,9,5,4,6,7,13,21,27,14,4,1];

plot(M,x_exp,'k*',M,P_exp,'r*');
print("nicholsonbailey_burnett.eps", "-deps")
hold off;

```

1.4 Some Useful 2D Plots

OCTAVE offers nice possibilities for 2D plots, we can use them easily e.g. for plotting 2D vector fields (arising from 2D ODE models). A basic code for the example of the Lotka Volterra predator prey model (2.6), (2.7) is

```
[x,y] = meshgrid(0:0.15:2);
xlabel('x (Prey) ');
hold on
ylabel('y (Predator)');
hold on
quiver (x, y, x-1.5.*x.*y, -y+x.*y,1.5, 'k');
% Save the figure
print("vector_predprey_LV.eps", "-depsc")
```

the resulting figure is shown in Fig. 2.26.

Invariants of motion can be easily plotted by using the command “contour”, again for the example of Lotka Volterra predator prey model (2.6), (2.7):

```
% Plot of level curves for the invariant of motion
% of the Lotka-Volterra Predator-prey model

[x,y]=meshgrid(linspace(0.1,3,50),linspace(0.1,3,50));
z = -x+log(x)+log(y)-1.5.*y;
xlabel('x (Prey) ');
hold on
ylabel('y (Predator)');
hold on
contour ( x,y,z,20)
print("contour_predprey_LV.eps", "-depsc")
```

the resulting figure is shown in Fig. 2.27.

2 Solutions

2.1 Computation of the steady state \bar{x} :

$$x_t = x_{t+1} \Leftrightarrow x_t = \frac{\lambda}{\alpha} x_t^{1-b}$$

$$\Leftrightarrow \bar{x} = 0 \text{ or } \bar{x} = \left(\frac{\lambda}{\alpha}\right)^{\frac{1}{b}}.$$

Let $f(x) = \frac{\lambda}{\alpha} x^{1-b}$, then

$$f'(x) = \frac{\lambda}{\alpha} (1-b)x^{-b},$$

and

$$f'\left(\frac{\lambda}{\alpha}\right) = 1-b.$$

The stability condition is satisfied if

$$|1-b| < 1 \Leftrightarrow 0 < b < 2.$$

Interpretation:

We consider the model in a “splitted way”:

$$x_{t+1} = \left(\frac{1}{\alpha} x_t^{-b}\right) (\lambda x_t),$$

the first factor denotes the survivorship, the second the progeny. For $b = 0$, the survivorship is not density-dependent and the system loses the stability of the steady state. For $b > 2$, one could say that the density-dependence is somehow too strong and thus destabilises the system.

2.2

(a) r denotes the basic reproduction rate; we can understand this fact denoting

$$g(x) = \frac{r}{1 + x(r-1)/K} x.$$

and computing $g'(0) = r$; the term $1/(1 + x(r-1)/K)$ indicates the survival probability. That r appears in the survival probability has merely technical reasons (as we will see). A reparametrisation of K can hide the parameter r in this term ($\tilde{K} = (r-1)/K$).

(b) Define $y_n = 1/x_n$, following the hint in the exercise. Then,

$$\begin{aligned} x_{n+1} &= \frac{r}{1 + x_n(r-1)/K} x_n \\ y_{n+1} &= (1 + x_n(r-1)/K) \frac{1}{rx_n} = \frac{1}{rx_n} + \frac{r-1}{rK} \\ &= \frac{1}{r} y_n + \frac{r-1}{rK} \end{aligned}$$

$$\begin{aligned}
&= \frac{1}{r^2} y_{n-1} + \left(\frac{1}{r} + 1 \right) \frac{r-1}{rK} \\
&= \frac{1}{r^3} y_{n-2} + \left(\frac{1}{r^2} + \frac{1}{r} + 1 \right) \frac{r-1}{rK} \\
&\vdots \\
&= \frac{1}{r^{n+1}} y_0 + \left(\sum_{i=0}^n \frac{1}{r^i} \right) \frac{r-1}{rK} \\
&= \frac{1}{r^{n+1}} y_0 + \frac{1 - (1/r)^{n+1}}{1 - 1/r} \frac{r-1}{rK} \\
&= \frac{1}{r^{n+1}} y_0 + \frac{r}{r^{n+1}} \frac{r^{n+1} - 1}{r-1} \frac{r-1}{rK} \\
&= \frac{1}{r^{n+1}} y_0 + \frac{1}{r^{n+1}} \frac{r^{n+1} - 1}{K}.
\end{aligned}$$

Thus, (note, that we now consider x_n and before y_{n+1} s.t. the index is shifted)

$$x_n = \frac{1}{\frac{1}{r^n} y_0 + \frac{1}{r^n} \frac{r^n - 1}{K}} = \frac{1}{1 + \frac{r^n - 1}{y_0 K}} \frac{1}{y_0 / r^n} = \frac{r^n x_0}{1 + \frac{r^n - 1}{K} x_0}.$$

Remark The Beverton-Holt model is the time-one map of the time-continuous logistic equation. Thus, the solution converges monotonously to the carrying capacity; no bifurcations may happen.

2.3 Since the transformation $y = x/K$ removes K from the model, stability solely depends on r . The non-trivial steady state reads

$$1 = re^{-\bar{x}} \quad \Rightarrow \quad \bar{x} = \ln(r).$$

The derivative of the r.h.s. at this stationary state is given by

$$f'(\bar{x}) = re^{-\bar{x}} - r\bar{x}e^{-\bar{x}} = 1 - \ln(r).$$

This stationary state is locally stable for $r > 1$ and $r < e^2 \approx 7.38$. Hence, we expect the wasp population to tend to an equilibrium (only perturbed by external factors as weather conditions etc.). This result can be also read off from Fig. 2.8.

2.4

(a) We have a priori that $0 \leq X_t \leq N$. Thus

$$\begin{aligned}
P(X_{t+\Delta t} = 0 | X_t = k) &\geq P(\text{no births due to } k \text{ individuals in } [t, t + \Delta t] \\
&\quad \text{and } k \text{ individuals die})
\end{aligned}$$

$$\begin{aligned}
&= \left[P(\text{no births due to one individual in } [t, t + \Delta t]) \right. \\
&\quad \left. P(\text{one individual dies in } [t, t + \Delta t]) \right]^k \\
&= \left[(1 - \beta\Delta t + o(\Delta t))(\mu\Delta t + o(\Delta t)) \right]^k \\
&= \tilde{\varepsilon}(\Delta t)^k
\end{aligned}$$

If Δt is sufficiently small, we find $1 > \tilde{\varepsilon}(\Delta t) > 0$, s.t.

$$P(X_{t+\Delta t} = 0 | X_t = k) \geq \tilde{\varepsilon}(\Delta t)^k \geq \tilde{\varepsilon}(\Delta t)^N =: \varepsilon.$$

(b) Let

$$p_l =: P(\text{Population extinct at time } t = l\Delta t).$$

Then,

$$\begin{aligned}
p_l &\geq P(X_{l\Delta} = 0 | X_{(l-1)\Delta} > 0) P(X_{(l-1)\Delta} > 0) + P(X_{l\Delta} = 0 | X_{(l-1)\Delta} = 0) \\
&\quad P(X_{(l-1)\Delta} = 0) \\
&= P(\text{Pop. goes extinct in } [(l-1)\Delta t, l\Delta t]) P(\text{Pop. not extinct at } t = (l-1)\Delta t) \\
&\quad + P(\text{Pop. extinct at } t = (l-1)\Delta t) \\
&\geq \varepsilon(1 - p_{l-1}) + p_{l-1} = \varepsilon + (1 - \varepsilon)p_{l-1}.
\end{aligned}$$

Now define the recursion

$$\tilde{p}_l = \varepsilon + (1 - \varepsilon)\tilde{p}_{l-1}.$$

and $\tilde{p}_0 = p_0 = 1$. Since

$$(p_l - \tilde{p}_l) \geq (1 - \varepsilon)(p_{l-1} - \tilde{p}_{l-1})$$

we find from $p_0 - \tilde{p}_0 \geq 0$ per induction that $p_l - \tilde{p}_l \geq 0$, i.e.

$$p_l \geq \tilde{p}_l.$$

(c) In the last step, we show that $\tilde{p}_l \rightarrow 1$ for $l \rightarrow \infty$. Since the function $f(x) = \varepsilon + (1 - \varepsilon)x$ maps the interval $[0, 1]$ into itself,

$$f([0, 1]) \subset [0, 1]$$

and $f'(x) < 1$ (i.e., $f(x)$ is a contraction), the iteration tends to a fixed point. The only fixed point of $f(x)$ is $x = 1$. Thus,

$$\tilde{p}_l \rightarrow 1 \quad \text{for } l \rightarrow \infty$$

and since $\tilde{p}_l \leq p_l \leq 1$, we also have

$$p_l \rightarrow 1 \quad \text{for } l \rightarrow \infty.$$

2.5

- (a) Consider $E = 0$; then, there is a maximal carrying capacity $x = K$; furthermore, let $f(x) = \alpha x \ln(K/x)$. Then, $f'(0) = \infty$. This is, a small population will rapidly (arbitrary fast) reproduce.
- (b) Stationary states: either $x = 0$ (which is possible as $\ln(x)x \rightarrow 0$ for $x \rightarrow 0$) or $x \neq 0$, corresponding to

$$\ln(K/x) = qE/\alpha \quad \Leftrightarrow \quad x = Ke^{-qE/\alpha}.$$

The yield curve is given by

$$Y(E) = qEK e^{-qE/\alpha}$$

with a maximal sustainable yield at

$$0 = Y'(E^*) = qKe^{-qE^*/\alpha}(1 - qE^*/\alpha) \quad \Leftrightarrow \quad E^* = \alpha/q.$$

It is remarkable that the capacity K does not play a role.

2.6 Model: $\dot{x} = rx \left(\frac{x}{K_0} - 1 \right) \left(1 - \frac{x}{K} \right) - qEx$.

- (a) K_0 indicates the minimal population size that is necessary for the population to survive.
- (b) Equilibria: $x = 0$ or (if $x \neq 0$)

$$\begin{aligned} 0 &= -x^2/(K_0 K) + x(1/K + 1/K_0) - 1 - qE/r \\ \Leftrightarrow \quad 0 &= x^2 - x(K + K_0) + K_0 K + qEK_0 K / r \\ \Leftrightarrow \quad x_{\pm} &= \frac{1}{2} \left(K + K_0 \pm \sqrt{(K + K_0)^2 - 4(K_0 K + qEK_0 K / r)} \right) \\ &= \frac{1}{2} \left(K + K_0 \pm \sqrt{(K - K_0)^2 - 4qEK_0 K / r} \right). \end{aligned}$$

(c) We find a saddle-node bifurcation at

$$E = \frac{(K - K_0)^2 r}{4qKK_0}.$$

That means, we must not bring the population below the average between the minimal and the maximal capacity, i.e., below $(K + K_0)/2$.

2.7 Assume inhabitable patches are converted into habitable patches at rate α , and habitable patches into inhabitable patches at rate μ . Then,

$$\begin{aligned} p'_0 &= \mu(p_1 + p_2) - \alpha p_0 \\ p'_1 &= -c(\rho)(1 - p_2(t)) + e(\rho)p_2(t) - \mu p_1 + \alpha p_0 \\ p'_2 &= c(\rho)(1 - p_2(t)) - e(\rho)p_2(t) - \mu p_2 \end{aligned}$$

In order to reduce this system to two dimensions, we use $p_0 + p_1 + p_2 = \text{constant}$. Since p_i are fractions, we may even assume $p_0 + p_1 + p_2 = 1$.

It is desirable to work with two dimensional systems, as more tools are available than for three or higher dimensional systems (Poincaré-Bendixson, negative criterion etc.); Moreover, the phase plane of a two-dimensional system is ready to visualise.

2.8 If $c_u c_v \neq 1$, then there may exist a fixed point in the interior of the positive quadrant. Condition for a fixed point:

$$u_{t+1} = u_t \quad \text{and} \quad v_{t+1} = v_t$$

which is equivalent to

$$1 = (u_t + c_v v_t)/K_u \quad \text{and} \quad 1 = (c_u u_t + v_t)/K_v.$$

This leads to

$$u_t = K_u - c_v v_t \quad \text{and} \quad v_t = K_v - c_u u_t.$$

By substitution we get

$$\begin{aligned} u_t &= K_u - c_v(K_v - c_u u_t) \\ \Leftrightarrow (1 - c_v c_u)u_t &= K_u - c_v K_v \\ \Leftrightarrow u_t &= \frac{K_u - c_v K_v}{1 - c_u c_v} \end{aligned}$$

and

$$\begin{aligned} v_t &= K_v - c_u \frac{K_u - c_v K_v}{1 - c_u c_v} \\ &= \frac{K_v - c_u c_v K_v}{1 - c_u c_v} - \frac{c_u K_u - c_u c_v K_v}{1 - c_u c_v} = \frac{K_v - c_u K_u}{1 - c_u c_v}. \end{aligned}$$

Hence the fixed point coordinates are

$$(e_u, e_v) = \left(\frac{K_u - c_v K_v}{1 - c_u c_v}, \frac{K_v - c_u K_u}{1 - c_u c_v} \right).$$

We will assume $K_u > c_v K_v$ and that $K_v > c_u K_u$, which in turn implies that $1 > c_u c_v$.

Let

$$f(u_t, v_t) = u_t e^{r_u(1-(u_t+c_v v_t)/K_u)}$$

$$g(u_t, v_t) = v_t e^{r_v(1-(c_u u_t+v_t)/K_v)}.$$

Computation of the Jacobian matrix (for the linearised system):

$$\begin{aligned} \frac{\partial f}{\partial u_t} &= a_{11} = e^{r_u(1-(u_t+c_v v_t)/K_u)} + u_t e^{r_u(1-(u_t+c_v v_t)/K_u)} \cdot \left(-\frac{r_u}{K_u} \right) \\ &= e^{r_u(1-(u_t+c_v v_t)/K_u)} \cdot \left(1 - \frac{r_u}{K_u} u_t \right) \\ \frac{\partial f}{\partial v_t} &= a_{12} = u_t e^{r_u(1-(u_t+c_v v_t)/K_u)} \cdot \left(-\frac{r_u c_v}{K_u} \right) \\ \frac{\partial g}{\partial u_t} &= a_{21} = v_t e^{r_v(1-(c_u u_t+v_t)/K_v)} \cdot \left(-\frac{r_v c_u}{K_v} \right) \\ \frac{\partial g}{\partial v_t} &= a_{22} = e^{r_v(1-(c_u u_t+v_t)/K_v)} \cdot \left(1 - \frac{r_v}{K_v} v_t \right). \end{aligned}$$

This has to be used at the stationary point (= fixed point). Using the model equations, we come to

$$\begin{aligned} a_{11} &= 1 - \frac{r_u}{K_u} u_t, \quad a_{12} = -\frac{r_u c_v}{K_u} u_t \\ a_{21} &= -\frac{r_v c_u}{K_v} v_t, \quad a_{22} = 1 - \frac{r_v}{K_v} v_t. \end{aligned}$$

Inserting the coordinates of the stationary point yields

$$\begin{aligned} a_{11} &= 1 - \frac{r_u}{K_u} e_u = 1 - \frac{r_u}{K_u} \left(\frac{K_u - c_v K_v}{1 - c_u c_v} \right) \\ a_{12} &= -\frac{r_u c_v}{K_u} e_u = -\frac{r_u c_v}{K_u} \left(\frac{K_u - c_v K_v}{1 - c_u c_v} \right) \\ a_{21} &= -\frac{r_v c_u}{K_v} e_v = -\frac{r_v c_u}{K_v} \left(\frac{K_v - c_u K_u}{1 - c_u c_v} \right) \\ a_{22} &= 1 - \frac{r_v}{K_v} e_v = 1 - \frac{r_v}{K_v} \left(\frac{K_v - c_u K_u}{1 - c_u c_v} \right). \end{aligned}$$

Let $A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix}$. Now we look for the eigenvalues of the matrix A .

$$\begin{aligned} &\left(1 - \frac{r_u}{K_u} e_u - \lambda\right) \cdot \left(1 - \frac{r_v}{K_v} e_v - \lambda\right) - \frac{r_u c_v}{K_u} e_u \cdot \frac{r_v c_u}{K_v} e_v = 0 \\ \Leftrightarrow &\left(1 - \frac{r_u}{K_u} e_u\right) \cdot \left(1 - \frac{r_v}{K_v} e_v\right) - \left(1 - \frac{r_v}{K_v} e_v + 1 - \frac{r_u}{K_u} e_u\right) \lambda + \lambda^2 - \frac{r_u r_v c_u c_v}{K_u K_v} e_u e_v = 0 \\ \Leftrightarrow &1 - \frac{r_v}{K_v} e_v - \frac{r_u}{K_u} e_u + \frac{r_u r_v}{K_u K_v} e_u e_v - \frac{r_u r_v c_u c_v}{K_u K_v} e_u e_v - \left(2 - \frac{r_u}{K_u} e_u - \frac{r_v}{K_v} e_v\right) \lambda + \lambda^2 = 0 \\ \Leftrightarrow &\lambda^2 + \left(\frac{r_u}{K_u} e_u + \frac{r_v}{K_v} e_v - 2\right) \lambda + \left(1 - \frac{r_v}{K_v} e_v - \frac{r_u}{K_u} e_u + \frac{r_u r_v}{K_u K_v} e_u e_v (1 - c_u c_v)\right) = 0, \end{aligned}$$

hence

$$\begin{aligned} \lambda_{1,2} &= -\frac{1}{2} \left(\frac{r_u}{K_u} e_u + \frac{r_v}{K_v} e_v - 2 \right) \\ &\quad \pm \frac{1}{2} \sqrt{\left(\frac{r_u}{K_u} e_u + \frac{r_v}{K_v} e_v - 2 \right)^2 - 4 \left(1 - \frac{r_v}{K_v} e_v - \frac{r_u}{K_u} e_u + \frac{r_u r_v}{K_u K_v} e_u e_v (1 - c_u c_v) \right)} \\ &= -\frac{1}{2} \left(\frac{r_u}{K_u} e_u + \frac{r_v}{K_v} e_v - 2 \right) \pm \frac{1}{2} \sqrt{\frac{r_u^2}{K_u^2} e_u^2 - 2 \frac{r_u r_v}{K_u K_v} e_u e_v + \frac{r_v^2}{K_v^2} e_v^2 + 4 \frac{r_u r_v c_u c_v}{K_u K_v} e_u e_v} \\ &= -\frac{1}{2} \left(\frac{r_u}{K_u} e_u + \frac{r_v}{K_v} e_v - 2 \right) \pm \frac{1}{2} \sqrt{\left(\frac{r_u}{K_u} e_u - \frac{r_v}{K_v} e_v \right)^2 + 4 \frac{r_u r_v c_u c_v}{K_u K_v} e_u e_v}. \end{aligned}$$

Let $a = \frac{r_u}{K_u} e_u$, $b = \frac{r_v}{K_v} e_v$, $c = c_u c_v$, yielding

$$\lambda_{1,2} = -\frac{1}{2}(a + b - 2) \pm \frac{1}{2} \sqrt{(a - b)^2 + 4abc}.$$

Do both eigenvalues lie inside the unit circle in the complex plane?

Due to $c < 1$ we get

$$\sqrt{(a-b)^2 + 4abc} = \sqrt{(a+b)^2 - 4ab + 4abc} \leq \sqrt{(a+b)^2} = a+b,$$

therefore $\lambda_1 < 1$ and $\lambda_2 > -\frac{1}{2}(a+b) + 1 - \frac{1}{2}(a+b) = -(a+b) + 1$. That means that the fixed point is asymptotically stable if

$$a+b < 2 \Leftrightarrow \frac{r_u}{K_u}e_u + \frac{r_v}{K_v}e_v < 2.$$

2.9 Interpretation of the terms:

- $x_1(1-x_2)$, $ax_2(1-x_2)$: limited growth of a single species, according to Verhulst (logistic growth)
- $b_1x_1x_2$, $b_2x_1x_2$: symbiosis terms (but survival possible without other species)

Computation of the stationary solutions:

$$\dot{x}_1 = 0 \Leftrightarrow x_1(1-x_1+b_1x_2) = 0 \Leftrightarrow x_1 = 0 \text{ or } x_1 = 1 + b_1x_2.$$

$$\dot{x}_2 = 0 \Leftrightarrow ax_2(1-x_2 + \frac{b_2}{a}x_1) = 0 \Leftrightarrow x_2 = 0 \text{ or } x_2 = 1 + \frac{b_2}{a}x_1.$$

\leadsto stationary points are $(0, 0)$, $(0, 1)$, $(1, 0)$, coexistence point:

$$x_1 = 1 + b_1 \left(1 + \frac{b_2}{a}x_1 \right) = 1 + b_1 + \frac{b_1b_2}{a}x_1$$

$$\Leftrightarrow \left(1 - \frac{b_1b_2}{a} \right) x_1 = 1 + b_1$$

$$\Leftrightarrow x_1 = \frac{1+b_1}{1-b_1b_2/a} < 0 \quad \text{for } b_1b_2/a < 1$$

and

$$x_2 = 1 + b_2(1 + b_1x_2) = 1 + \frac{b_2}{a} + \frac{b_1b_2}{a}x_2$$

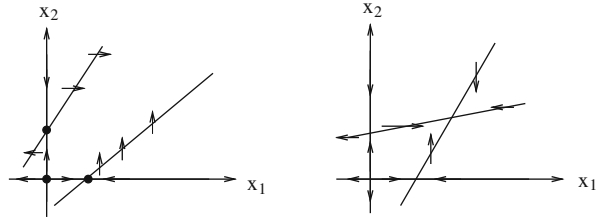
$$\Leftrightarrow \left(1 - \frac{b_1b_2}{a} \right) x_2 = 1 + \frac{b_2}{a}$$

$$\Leftrightarrow x_2 = \frac{1+b_2/a}{1-b_1b_2/a} > 0 \quad \text{for } b_1b_2/a < 1$$

The position of the stationary points and the isoclines are shown in Fig. 2.53. The Jacobian matrix reads:

$$J = \begin{pmatrix} 1 - 2u_1 + b_1u_2 & b_1u_1 \\ b_2u_2 & a - 2au_2 + b_2u_1 \end{pmatrix},$$

Fig. 2.53 *Left:* case $b_1 b_2 / a > 1 \Leftrightarrow \frac{1}{b_1} < \frac{b_2}{a}$,
right: case $b_1 b_2 / a < 1$



respectively in the stationary points:

- $J(0, 0) = \begin{pmatrix} 1 & 0 \\ 0 & a \end{pmatrix} \leadsto$ unstable node
- $J(0, 1) = \begin{pmatrix} 1 + b_1 & 0 \\ b_2 & -a \end{pmatrix} \leadsto \det J < 0 \leadsto$ saddle
- $J(1, 0) = \begin{pmatrix} -1 & b_1 \\ 0 & a + b_2 \end{pmatrix} \leadsto \det J < 0 \leadsto$ saddle
- Consider this stationary point only in the case of coexistence, i.e., $b_1 b_2 / a < 1$:

$$\begin{aligned}
 J\left(\frac{1+b_1}{1-b_1 b_2/a}, \frac{1+b_2/a}{1-b_1 b_2/a}\right) &= \begin{pmatrix} 1 + \frac{-2-2b_1+b_1+b_1 b_2/a}{1-b_1 b_2/a} & \frac{b_1(1+b_1)}{1-b_1 b_2/a} \\ \frac{b_2(1+b_2/a)}{1-b_1 b_2/a} & a + \frac{-2a-2b_2+b_2+b_1 b_2}{1-b_1 b_2/a} \end{pmatrix} \\
 &= \begin{pmatrix} \frac{1-b_1 b_2/a-2-b_1+b_1 b_2/a}{1-b_1 b_2/a} & \frac{b_1(1+b_1)}{1-b_1 b_2/a} \\ \frac{b_2(1+b_2/a)}{1-b_1 b_2/a} & \frac{a-b_1 b_2-2a-b_2+b_1 b_2}{1-b_1 b_2/a} \end{pmatrix} \\
 &= \begin{pmatrix} \frac{-1-b_1}{1-b_1 b_2/a} & \frac{b_1(1+b_1)}{1-b_1 b_2/a} \\ \frac{b_2(1+b_2/a)}{1-b_1 b_2/a} & \frac{-a-b_2}{1-b_1 b_2/a} \end{pmatrix}.
 \end{aligned}$$

Since

$$\begin{aligned}
 a + b_2 - b_1 b_2 \left(1 + \frac{b_2}{a}\right) &> a + b_2 - b_1 b_2 \left(1 + \frac{1}{b_1}\right) \\
 &= a + b_2 - b_1 b_2 - b_2 \\
 &= a - b_1 b_2 > 0
 \end{aligned}$$

this yields

$$\begin{aligned}
 \det J &= \frac{1+b_1}{(1-b_1 b_2/a)^2} \cdot \left[a + b_2 - b_1 b_2 - \frac{b_1 b_2^2}{a} \right] > 0 \\
 \operatorname{tr} J &= \frac{1}{(1-b_1 b_2/a)} [-1 - b_1 - a - b_2] < 0,
 \end{aligned}$$

which means that the coexistence point is stable.

2.10 Model:

$$\dot{x} = -\alpha x + \beta xy$$

$$\dot{y} = -\gamma y + \delta xy$$

- (a) Both species die without the other species; reproduction is only possible by means of the help of the opposite species. This model could be viewed as a simple two-sex model.
- (b) Stationary points: trivial stationary point, $(0, 0)$. If $x \neq 0 \leadsto y \neq 0$ and vice versa. Non-trivial stationary point is solution of the linear system

$$0 = -\alpha + \beta y$$

$$0 = -\gamma + \delta x$$

i.e., $y^* = \alpha/\beta$, $x^* = \gamma/\delta$.

General Jacobian at (x, y) :

$$J = \begin{pmatrix} -\alpha + \beta y & \beta x \\ \delta y & -\gamma + \delta x \end{pmatrix}.$$

Trivial stationary point $(0, 0)$:

$$J = \begin{pmatrix} -\alpha & 0 \\ 0 & -\gamma \end{pmatrix} \Rightarrow \lambda_1 = -\alpha < 0, \lambda_2 = -\gamma < 0 \Rightarrow \text{stable node.}$$

Coexistence point (x^*, y^*) :

$$J = \begin{pmatrix} 0 & \beta\gamma/\delta \\ \delta\alpha/\beta & 0 \end{pmatrix} \Rightarrow \text{tr}(J) = 0, \det(J) = -\alpha\gamma < 0 \Rightarrow \text{saddle.}$$

Sketch: See Fig. 2.54.

- (c) If there are not enough members of one (or both) species, the cooperation effect is too small to keep them alive. If the population size of both species exceed a certain threshold, the population grows unbounded. A carrying capacity or alike is missing.

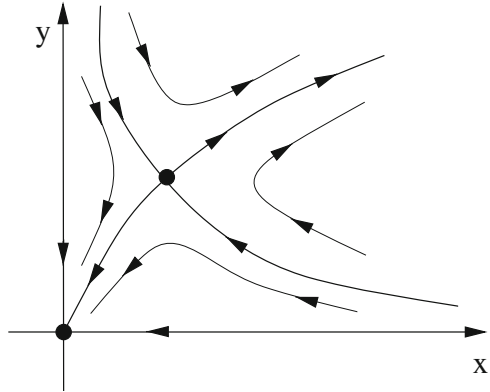
2.11 Model:

$$\dot{x}_1 = x_1(1 - x_1 - \alpha x_2 - \beta x_3)$$

$$\dot{x}_2 = x_2(1 - x_2 - \alpha x_3 - \beta x_1)$$

$$\dot{x}_3 = x_3(1 - x_3 - \alpha x_1 - \beta x_2).$$

Fig. 2.54 Sketch of the phase plane given in Exercise 2.10



- (a) For a given species, the presence of the other species leads to a decrease of the carrying capacity.
- (b) Stationary points:
- Trivial stationary point $(0, 0, 0)$
 - One species only: $(1, 0, 0)$, $(0, 1, 0)$, $(0, 0, 1)$
 - Two species only; start with $x_3 = 0$:

$$\begin{pmatrix} 1 & \alpha \\ \beta & 1 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \end{pmatrix} \Rightarrow \begin{pmatrix} x_1 \\ x_2 \end{pmatrix} = \frac{1}{1 - \alpha\beta} \begin{pmatrix} 1 - \alpha \\ 1 - \beta \end{pmatrix}.$$

From symmetry reasons, we find three stationary points with two species,

$$(1 - \alpha, 1 - \beta, 0)/(1 - \alpha\beta), \quad (1 - \beta, 0, 1 - \alpha)/(1 - \alpha\beta), \quad (0, 1 - \alpha, 1 - \beta)/(1 - \alpha\beta).$$

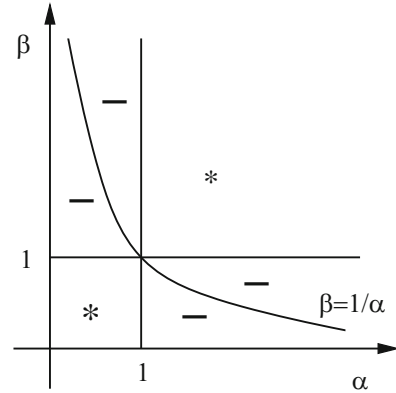
- Coexistence point: (for symmetry reasons, we find $x_1 = x_2 = x_3$):

$$\begin{pmatrix} 1 & \alpha & \beta \\ \beta & 1 & \alpha \\ \alpha & \beta & 1 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} = \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix} \Rightarrow \begin{pmatrix} x_1 \\ x_2 \\ x_3 \end{pmatrix} = \frac{1}{1 + \alpha + \beta} \begin{pmatrix} 1 \\ 1 \\ 1 \end{pmatrix}$$

Looking at stationary points only (no stability analysis), we expect all three species to be coexistent for all non-negative α, β ; the two-species solution are within the positive cone if

$$(1 - \alpha)/(1 - \alpha\beta) > 0, \quad (1 - \beta)/(1 - \alpha\beta) > 0.$$

Fig. 2.55 Existence of feasible two-species stationary points (stability not considered). The regions marked with a *star* allow for two-species solutions. Exercise 2.11



We find six different cases, depicted in Fig. 2.55. The present model can be interpreted as a special, highly symmetric case of Volterra's competition model.

2.12 Model: (phytoplankton P , nitrogen N , zooplankton Z)

$$\dot{N} = aP + bZ - cNP$$

$$\dot{P} = cNP - dPZ - aP$$

$$\dot{Z} = dPZ - bZ.$$

- (a) The equations satisfy obviously $\dot{N} + \dot{P} + \dot{Z} = 0$, so the mass of nitrogen is conserved, $N + P + Z = A (= \text{const})$.
- (b) From the third equation we get: $Z = 0$ or $P = b/d$. The second equation yields $P = 0$ or $N = (dZ + a)/c$. Furthermore, the conservation equation holds, i.e. $A = N + Z + P$. Thus, there are three possibilities to satisfy all three stationary equations at once:

$Z = 0$ and $P = 0$, thus $N = A - Z - P = A$, i.e., $S_0 = (A, 0, 0)$

$Z = 0$ and $N = (dZ + a)/c = a/c$, $P = A - Z - N = A + a/c$, i.e. $S_1 = (a/c, A + a/c, 0)$

$P = b/d$, $Z = (cN - a)/d$, $N = A - P - Z$, thus $Z = c/(d + c)(A - b/d - a/c)$ and $N = A - b/d - c/(d + c)(A - b/d - a/c)$, i.e., $S_2 = (A - b/d - c/(d + c)(A - b/d - a/c), b/d, c/(d + c)(A - b/d - a/c))$.

Remark that P (the corresponding coordinate of the stationary point S_2) is independent of A , this means biologically that not the phytoplankton, but only the zooplankton benefits from an increased level of nitrogen, a typical behaviour in a food chain.

- (c) Parameter c describes the uptake rate of nitrogen, which may vary over the seasons. The general Jacobian matrix reads

$$J = \begin{pmatrix} -cP & a - cN & b \\ cP & cN - dZ - a & -dP \\ 0 & dZ & dP - b \end{pmatrix}$$

In the stationary points:

$$J(S_0) = \begin{pmatrix} 0 & a - cA & b \\ 0 & cA - a & 0 \\ 0 & 0 & -b \end{pmatrix},$$

with the eigenvalues $\lambda_1 = 0$, $\lambda_2 = cA - a$, $\lambda_3 = -b$.

$$J(S_1) = \begin{pmatrix} -cA + a & 0 & b \\ cA - a & 0 & -dA + \frac{da}{c} \\ 0 & 0 & dA - \frac{da}{c} - b \end{pmatrix},$$

with the eigenvalues $\lambda_1 = 0$, $\lambda_2 = -cA + a$, $\lambda_3 = dA - \frac{da}{c} - b$.

$$J(S_2) = \begin{pmatrix} -\frac{cb}{d} & a - \frac{c}{c+d}(d(A - \frac{b}{d}) + a) & b \\ \frac{cb}{d} & 0 & -b \\ 0 & d(A - \frac{b}{d} - \frac{1}{c+d}(d(A - \frac{b}{d}) + a)) & 0 \end{pmatrix},$$

with the eigenvalues $\lambda_{1,2} = -\frac{bc \pm \sqrt{b^2c^2 + 4d^2ba - 4d^2bAc + 4db^2c}}{2d}$, $\lambda_3 = 0$.

So, the qualitative behaviour of the system can be classified, dependent on c as follows:

Case 1: $c < \frac{a}{A}$ There is only S_0 in the biologically relevant area. The eigenvalues of the Jacobian matrix in S_0 are ≤ 0 . In S_1 , the Jacobian matrix has at least one positive eigenvalue and is thus unstable. Interpretation: The nitrogen uptake is not sufficient to keep a phytoplankton and furthermore a zooplankton population alive.

Case 1/2: $c = \frac{a}{A}$ S_0 and S_1 meet at $(A, 0, 0)$. In S_0 , the eigenvalue $\lambda_2 = cA - a$ crosses the 0 towards positive values (for increasing c), in S_1 , the eigenvalue $\lambda_2 = -cA + a$ crosses the 0 towards negative values (and $\lambda_3 = dA - \frac{da}{c} - b < 0$ is sure), so S_0 loses its stability, becoming a saddle, while S_1 gains stability; thus a transcritical bifurcation!

Case 2: $c > \frac{a}{A}$, and $c < \frac{a}{A - \frac{b}{d}}$ S_0 yields at least one positive eigenvalue and thus is unstable. S_1 has all eigenvalues ≤ 0 and is taken to be stable here. Interpretation: The nitrogen uptake is higher, allowing the existence of a non-zero phytoplankton

population; but the level of the phytoplankton is still not sufficient to keep the zooplankton population on a non-zero level.

Case 2/3: $c = \frac{a}{A + \frac{b}{d}}$ S_1 and S_2 meet at $(A - \frac{b}{d}, \frac{b}{d}, 0)$; the eigenvalue $\lambda_3 = dA - \frac{da}{c} - b$ of the Jacobian matrix in S_1 crosses the 0 towards positive values, thus S_1 loses stability, becoming a saddle; at the same time, the positive eigenvalue in S_2 crosses the 0 towards negative values, so S_2 gains stability; thus another transcritical bifurcation.

Case 3: $c > \frac{a}{A + \frac{b}{d}}$ S_0 is unstable, S_1 is unstable, S_2 has all eigenvalues ≤ 0 and thus assumed to be stable here. Interpretation: Now the nitrogen uptake of the phytoplankton is so high that it is sufficient to keep phytoplankton and zooplankton alive.

2.13 Model: $\dot{x} = rx \left(1 - \frac{x}{K}\right) - \frac{x^2}{1+x^2}$, $K = 6$.

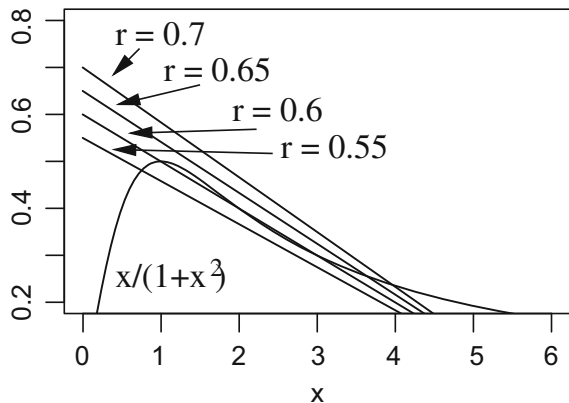
- (a) The term $-\frac{x^2}{1+x^2}$ represents predation on the budworms (mainly by birds).
- (b) Stationary points are given by $x = 0$, or

$$g(x) = r(1 - x/6) = \frac{x}{1+x^2} = h(x).$$

Depending on r , we may have one, three, or – in non-generic cases – also two intersection points, i.e., up to four stationary points (Fig. 2.56).

- (c) We find saddle-node bifurcations.
- (d) In the case of a lower r , there is also a lower level stationary state of x , which might allow to reduce the outbreak of the budworm significantly. A situation like that is called “bistable behaviour” – there are two stable stationary states, so it depends on the “history” to which stationary state a solution will tend to (Hysteresis).

Fig. 2.56 Intersections of $r(1 - x/6)$ (straight lines) and $x/(1 + x^2)$; Exercise 2.13



2.14 Model: (plants P , herbivores H)

$$\dot{P} = \phi - aP - bPH$$

$$\dot{H} = ebPH - cH.$$

- (a) Plant seed basically comes from outside the system and leads to a constant inflow into the plant compartment (ϕ). Plants die ($-aP$) and are nutrient for herbivores ($-bPH$). Herbivores die ($-cH$) and grow on plants $ebPH$, where e denotes a plant-biomass to herbivore-biomass conversion factor.

- (b) Trivial stationary state: $(P, H) = (\phi/a, 0)$

Non-trivial stationary state (with $H \neq 0$), $(P, H) = (c/(eb), (e\phi/c - a/b))$. It is typical that the energy available (ϕ) does not increase the plant population, but the highest tropic level, the herbivores.

Stability analysis: general Jacobian

$$J = \begin{pmatrix} -a - bH & -bP \\ ebH & ebP - c \end{pmatrix}.$$

Trivial stationary point:

$$J = \begin{pmatrix} -a & -b\phi/a \\ 0 & \phi eb/a - c \end{pmatrix} \Rightarrow \lambda_1 = -a, \lambda_2 = \phi eb/a - c.$$

Stable node for $\phi < ca/(eb)$, saddle point if $\phi > ca/(eb)$.

Non-trivial state:

$$J = \begin{pmatrix} \phi eb/c - a & -c/e \\ e(\phi eb/c - a) & 0 \end{pmatrix}.$$

Hence, $\text{tr}(J) = \phi eb/c - a$, $\det(J) = c(\phi eb/c - a)$. This stationary state is stable, if $\phi eb/c - a > 0$.

- (c) All in all, we find a transcritical bifurcation at $\phi_0 = ca/(eb)$; If $\phi < \phi_0$, not enough energy is in the system to carry also herbivores. For $\phi > \phi_0$, the coexistence point becomes non-negative and locally asymptotically stable.
- (d) A sketch of the phase plane can be found in Fig. 2.57.

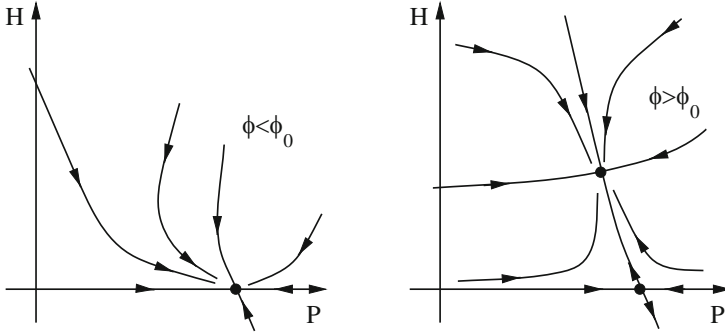


Fig. 2.57 Phase plane for $\phi < \phi_0$ (left) and $\phi > \phi_0$ (right); Exercise 2.14

2.15 Model: x_1, x_2 species, S Substrate,

$$\dot{x}_1(t) = x_1 \left(\frac{g_1 S(t)}{k_1 + S(t)} - m_1 \right)$$

$$\dot{x}_2(t) = x_2 \left(\frac{g_2 S(t)}{k_2 + S(t)} - m_2 \right)$$

$$\dot{S}(t) = D(S_0 - S(t)) - z_1 x_1 \frac{g_1 S(t)}{k_1 + S(t)} - z_2 x_2 \frac{g_2 S(t)}{k_2 + S(t)}$$

- (a) g_i, k_i specify the consumption of the substrate by species $i = 1, 2$. D : dilution rate, z_i : indicates the conversion from substrate to biomass, m_i : maintenance of bacteria (non-negative) and dilution, combined.

(b)

$$\dot{y}_1(t) = y_1 (f_1(S(t)) - m_1)$$

$$\dot{y}_2(t) = y_2 (f_2(S(t)) - m_2)$$

$$\dot{S}(t) = D(S_0 - S(t)) - y_1 f_1(S(t)) - y_2 f_2(S(t))$$

- (c) If we allowed to make any assumption, we take $m_1 = m_2 = D$ (dilution only), and find

$$\frac{d}{dt}(S + y_1 + y_2) = DS_0 - D(S + y_1 + y_2).$$

Asymptotically $S = S_0 - y_1 - y_2$ exponentially fast. We are allowed to replace S by this expression in order to investigate the long term behaviour ω -limit set

of this model,

$$\dot{y}_1(t) = y_1 (f_1(S_0 - y_1 - y_2) - D)$$

$$\dot{y}_2(t) = y_2 (f_2(S_0 - y_1 - y_2) - D).$$

(d) Scale the vector field by $1/(y_1 y_2)$. Negative criterion yields

$$\begin{aligned} & (f_1(S_0 - y_1 - y_2)/y_2 - D/y_2)_{y_1} + (f_2(S_0 - y_1 - y_2)/y_1 - D/y_1)_{y_2} \\ &= -f'_1(S_0 - y_1 - y_2)/y_2 - f'_2(S_0 - y_1 - y_2)/y_1 < 0 \end{aligned}$$

as $f'_i(S) > 0$. No periodic orbit is possible.

2.16

(a) First of all, we find as usual

$$\begin{aligned} (S_0 - (S + y))' &= -D(t)(S_0 - (S + y)) \\ \Rightarrow S_0 - (S(t + T) + y(t + T)) &= e^{-\int_0^T D(\tau) d\tau} (S_0 - (S(t) - y(t))). \end{aligned}$$

As $(\hat{y}(t), \hat{S}(t))$ is a T -periodic solution and $0 < \exp\left(-\int_0^T D(\tau) d\tau\right) < 1$, we obtain $S_0 - \hat{S}(t) - \hat{y}(t) = 0$. Thus, we may replace the ODE for $\hat{y}(t)$ by

$$\hat{y}' = -D(t)\hat{y} + h(\hat{y})$$

where

$$h(\hat{y}) = \hat{y}f(S_0 - \hat{y}).$$

Integrating this differential equation over one period (taking into account that $\hat{y}(0) = \hat{y}(T)$) yields

$$\langle D(t)\hat{y}(t) \rangle = \langle h(\hat{y}) \rangle.$$

(b) As $f'(\cdot) \geq 0 \geq f''(\cdot)$,

$$h''(x) = (f(S_0 - x) - xf'(S_0 - x))' = -2f'(S_0 - x) + xf''(S_0 - x) < 0$$

the function $h(\cdot)$ is convex. Thus, for $x_0 > 0$, $\Delta \in \mathbb{R}$ s.t. $x_0 + \Delta > 0$ we have

$$h(x_0 + \Delta) \leq h(x_0) + \Delta h'(x_0),$$

where equality is only given for $\Delta = 0$. Thus,

$$\begin{aligned} \langle h(\hat{y}) \rangle &= \langle h(\langle \hat{y} \rangle + (\hat{y} - \langle \hat{y} \rangle)) \rangle \leq \langle h(\langle \hat{y} \rangle) \\ &+ (\hat{y} - \langle \hat{y} \rangle)h'(\langle \hat{y} \rangle) \rangle = h(\langle \hat{y} \rangle) \end{aligned}$$

where equality only holds true if and only if $\hat{y}(t)$ is constant.

We assume that $\hat{S}(t), \hat{y}(t) \geq 0$. Due to $S_0 = \hat{S} + \hat{y}$, we have $\hat{y}(t) \in [0, S_0]$. Therefore,

$$\langle \hat{y} \rangle \in [0, S_0].$$

Case 1: If $\langle \hat{y} \rangle = 0$, choose a constant $d > f_\infty$. In this case, the only (and globally attractive) stationary solution is $y_0 = 0$, and thus $\langle y_0 \rangle = y_0 = 0$.

Case 2: If $\langle \hat{y} \rangle > 0$, choose

$$d = \frac{h(\langle \hat{y} \rangle)}{\langle \hat{y} \rangle},$$

then the non-trivial stationary point y_0 satisfies

$$0 = -dy_0 + h(y_0)$$

i.e.,

$$\langle dy_0 \rangle = h(y_0) = h(\langle y_0 \rangle) = h(\langle \hat{y} \rangle) \geq \langle h(\hat{y}) \rangle.$$

As we are able to move the gain to zero in a continuous way by increasing the dilution rate, we find a constant rate that exactly meets the average gain of the periodic case.

- (c) In the constant case, the optimal gain is given at a population level y^* where $h(y)$ assumes its maximum in $[0, S_0]$,

$$0 = h'(y^*) = f(S_0 - y^*) - y^*f'(S_0 - y^*).$$

As $h(y^*)$ function is strictly decreasing, there is a unique maximum. No non-trivial periodic dilution rate is able to meet this gain, as for any non-constant function $\hat{y}(t)$ we have the strict inequality

$$\langle h(\hat{y}) \rangle < h(\langle \hat{y} \rangle) \leq h(y^*).$$

2.17 As S_0, x and D is known, the unknown parameters are α and β . The data only describe the outcome in steady state conditions. Thus,

$$S = D/\alpha$$

and

$$S_0 = S + \beta x S / D = \frac{D}{\alpha} + \frac{\beta}{\alpha} x.$$

This equation can be viewed as a linear statistical model in the variables

$$A = 1/\alpha, \quad B = \beta/\alpha.$$

In R, the code reads

```
# data
S0 = c(10,10,1,1);
x = c(2.2*10**6, 2.2*10**4, 0.9*10**6, 0.8*10**5);
D = c(0.066, 0.044, 0.066, 0.044);

# linear model: S0 = A D+B x, no intercept.
res = lm(S0~D+x-1);
print(summary(res));
```

With this code, we obtain the result

```
Call:
lm(formula = S0 ~ D + x - 1)

Residuals:
    1     2     3     4 
2.089  6.775 -5.067 -2.307

Coefficients:
      Estimate Std. Error t value Pr(>|t|)
D  7.259e+01  9.148e+01   0.794   0.511
x  1.418e-06  4.314e-06   0.329   0.774

Residual standard error: 6.374 on 2 degrees of freedom
Multiple R-squared:  0.5977,    Adjusted R-squared:  0.1954 
F-statistic: 1.486 on 2 and 2 DF,  p-value: 0.4023
```

Of course, so little data will not lead to a precise estimation. Nevertheless, we find

$$A \approx 72.6 \text{ h mg/l}$$

i.e.,

$$\alpha \approx 0.014 \text{ l/(h mg)},$$

and

$$B \approx 1.418 \cdot 10^{-6} \text{ (mg/l)/(cells/l)} = 1.418 \cdot 10^{-6} \text{ (mg/cell)}.$$

The constant B tells us, how much nutrient is necessary to create one new cell. The constant B and α together yield β :

$$\beta \approx B\alpha = 1.598 \cdot 10^{-8} \text{ (1/h cells)}.$$

2.18 Without pesticides, we have a simple Lotka-Volterra-model: let x denote the prey, and y the predator we have (see Sect. 2.3.2.1)

$$\begin{aligned}\dot{x} &= ax - bxy \\ \dot{y} &= -dy + cxy.\end{aligned}$$

The stationary coexistence point, which is – on the same time – also the time average of the populations – thus reads

$$x = d/c, \quad y = \frac{a}{b}.$$

Now we add the effect of pesticides. We may have two consequences: either the pesticides only act at the pest level, or (as the predators take up the poison via their prey) also the predator population is affected. Let us assume that the poison does not drive the predator to extinction.

Possibility 1: The pesticide acts as an additional mortality (decreased growth rate) for the pest only,

$$\begin{aligned}\dot{x} &= (a - \delta)x - bxy \\ \dot{y} &= -dy + cxy.\end{aligned}$$

In this case the coexistence point is given by

$$x = d/c, \quad y = \frac{a - \delta}{b}.$$

This is, the pesticides, though killing the pest only, only affect the predators.

Possibility 2: The pesticide acts as an additional mortality (decreased growth rate) for pest and predator,

$$\begin{aligned}\dot{x} &= (a - \delta_1)x - bxy \\ \dot{y} &= -(d + \delta_2)y + cxy.\end{aligned}$$

The coexistence point is given by

$$x = (d + \delta_2)/c, \quad y = \frac{a - \delta_1}{b}.$$

In this case, the result is even worse than in the first modelling approach: by using pesticides, we may even increase the amount of pest.

This effect is called “the paradox of pesticides”. If we apply pesticides, we may increase the pest population unless we are not prepared to drive the higher trophic levels to extinction.

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