

Numerical bifurcation analysis of a tri-trophic food web with omnivory

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Abstract

We study the consequences of omnivory on the dynamic behaviour of a three species food web under chemostat conditions. The food web consists of a prey consuming a nutrient, a predator consuming a prey and an omnivore which preys on the predator and the prey. For each trophic level an ordinary differential equation describes the biomass density in the reactor. The hyperbolic functional response for single and multi prey species figures in the description of the trophic interactions. There are two limiting cases where the omnivore is a specialist; a food chain where the omnivore does not consume the prey and competition where the omnivore does not prey on the predator. We use bifurcation analysis to study the long-term dynamic behaviour for various degrees of omnivory. Attractors can be equilibria, limit cycles or chaotic behaviour depending on the control parameters of the chemostat. Often multiple attractor occur. In this paper we will discuss community assembly. That is, we analyze how the trophic structure of the food web evolves following invasion where a new invader is introduced one at the time. Generally, with an invasion, the invader settles itself and persists with all other species, however, the invader may also replace another species. We will show that the food web model has a global bifurcation, being a heteroclinic connection from a saddle equilibrium to a limit cycle of saddle type. This global bifurcation separates regions in the bifurcation diagram with different attractors to which the system evolves after invasion. To investigate the consequences of omnivory we will focus on invasion of the omnivore. This simplifies the analysis considerably, for the end-point of the assembly sequence is then unique. A weak interaction of the omnivore with the prey combined with a stronger interaction with the predator seems advantageous. © 2002 Elsevier Science Inc. All rights reserved.

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1. Introduction

There is an extended literature on the consequences of omnivory on the dynamical behaviour of food webs. This issue was studied both from the experimental, for instance in [1], and the theoretical point of view, see for instance [2]. Field data were used as well as manipulative experiments were performed. We will study omnivory by use of a mathematical model and bifurcation analysis thereof. We will assume that an abiotic nutrient is supplied to the system at a constant rate. The species leave the well mixed or spatially homogeneous environment because of death, harvesting, predation or emigration.

Many theoretical food web studies use the classical continuous-time Lotka–Volterra model [3], and focus the analysis on equilibria, positive biomasses and local stability. Law and Morton [4] take into account non-equilibrium long-term dynamic behaviour and use a global criterion for persistence of species. For a Lotka–Volterra model they derive an invasion criterion using the equilibrium values where the density of the invader is zero. Invasion is possible when the initial rate of increase of the new species is positive, irrespective whether the attractor of the virgin system is a fixed point, a periodic or a chaotic attractor. Diehl and Feißel [5] extend the Lotka–Volterra model by inclusion of omnivory. They use their model for numerical simulations to support conclusions from their experiments. They study enrichment on a tri-trophic food web with omnivory. The Lotka–Volterra model has the unrealistic property that feeding has no saturation.

The Rosenzweig–MacArthur model [6] often figures in theoretical analyses of food web dynamics. This model, which uses the Holling type II functional response to describe the trophic interactions, was initially proposed for a predator–prey system and later extended to a model for a three species prey–predator–top-predator food chain. A number of authors [7–10] have analyzed the long-term dynamics of this food chain using bifurcation analysis. McCann et al. [2,11] have extended this model with omnivory. They use a multi-species Holling type II functional response for the mathematical description of the omnivorous top-predator and both of its prey. The Rosenzweig–MacArthur model and the Lotka–Volterra model have the problem that no mass balance is provided.

In this paper we will study the dynamics of a three species food web including omnivory under chemostat conditions, using a mass balance model formulation in which the nutrient is modelled explicitly. The chemostat is the most commonly used system for ecological studies for aquatic habitats. The two control parameters, the dilution rate and the concentration substrate in the supply, are the natural bifurcation parameters. The parameter values base on data given in [12,13]. Both are studies on the dynamic behaviour of a microbial food chain consisting of substrate, bacterium and a ciliate in a chemostat. The authors show that the introduction of maintenance has a stabilizing effect, especially at low dilution rates. With the Marr–Pirt model, which takes into account maintenance, and for biologically plausible values, a cascade of period doubling leads to chaotic behaviour of a nutrient–prey–predator system. As in the bi-trophic Rosenzweig–MacArthur model, chaos is impossible for the Monod model, which considers no costs for maintenance. This has consequences for invisibility of this bi-trophic food chain. We show that a flip bifurcation in the absence of the omnivore continues smoothly into an interior flip bifurcation of the tri-trophic food web with omnivory. Furthermore, a cascade of these interior period doubling bifurcations gives chaotic behaviour of the prey–predator–omnivore system.

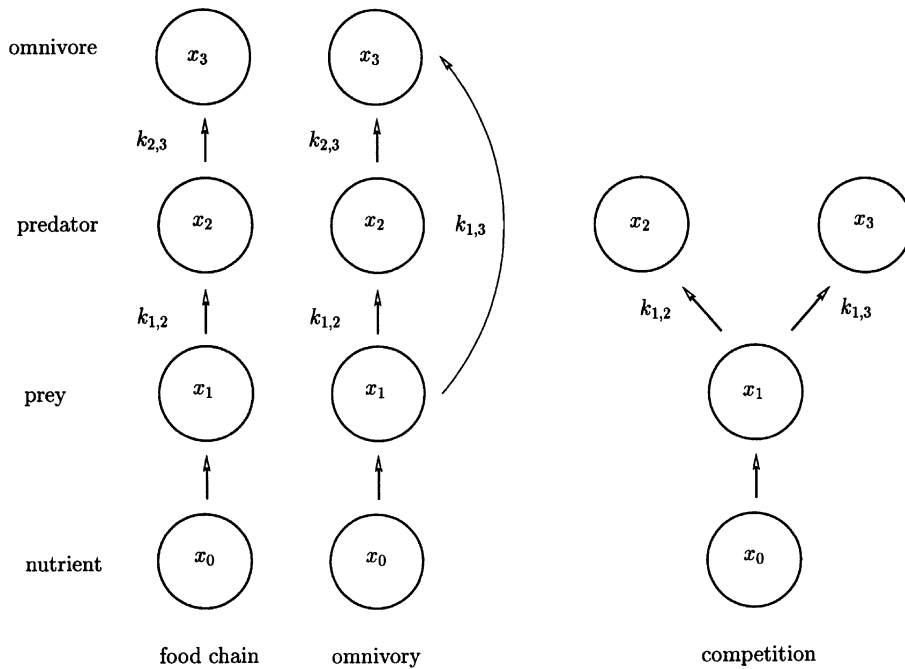


Fig. 1. Food web structure with biotic trophic levels, x_i , $i = 1, 2, 3$ and an abiotic nutrient, x_0 , at the base. The parameters $k_{1,3}$ and $k_{2,3}$ which fix in our study the trophic interactions are indicated. Left: food chain, omnivore x_3 consumes only predator x_2 . Middle: generalist omnivore x_3 consumes prey x_1 and predator x_2 . Right: competition, omnivore consumes only prey x_1 . The latter system was also studied in [19].

There are two limiting cases in which the omnivore acts as a specialist. Those are a food chain where the omnivore, then called top-predator, consumes only the predator, and competition where the omnivore, then called competitor, like the predator only consumes the prey species, Fig. 1. The food chain case has been discussed in previous papers [14–17] and in [18]. The competition limiting case has been studied extensively by Smith and Waltman in [19]. We expand on their work applying numerical bifurcation analysis.

A complete bifurcation analysis of natural, large-scale food webs is easy to imagine in principle. However, in practice it is not feasible because of the large number of state variables and parameters involved, notwithstanding the fact that fast computers and numerical bifurcation analysis software are currently available. Some of the parameters are specific for a species, such as maintenance rate, others are fixed by the trophic interactions, such as ingestion rate. When the trophic interactions are modelled with a Holling type II multi-species functional response multiple positive solutions are the rule, which complicates the analysis considerably.

To reduce the complexity of the problem we focus on a simple version of a community assembly, see [20]. Here only the three species are added to an existing food web under different, but time-invariant environmental conditions, starting with nutrients. The start is from a habitat where only abiotic nutrients are available, for instance a cleared lake, or a coral reef after extremely low tides or a cyclone. A species enters in small amounts, but nevertheless we assume no extinction due to demographic stochasticity. It can be investigated under which environmental conditions

this species can invade and settle. After this system converged to an attractor, a second species enters and invasibility is checked again, and so on. This simplifies the analysis considerably: invasion of a species one at a time limits the number of stable and invisible resistant end-points of a food web in which a steady community pattern is reached. However, replacement of the predator by the invading omnivore and visa versa, remains possible. We here study the assembly of an, admittedly less natural, but tractable small-scale (three species) food web in which the predator is introduced before the omnivore.

We study the influence of omnivory by performing a sensitivity analysis of the position of the codim-2 points in the two-parameter bifurcation diagram with respect to the parameters that define omnivory. These codim-2 points are the intersection point of codim-1 bifurcation curves that separate two-parameter bifurcation diagrams in regions with different asymptotic behaviour. We show that this approach gives a good insight in the consequences of varying a parameter on the long-term dynamics of the food web. Since the omnivore species enters into a system in which the predator species is already present, the end-point is unique. A measure for the success of the omnivore is the area in the bifurcation diagram with the environmental parameters as free parameters, which marks the parameter space where the end-point is coexistence of all species.

The results indicate that a weak interaction between the omnivore and the prey is advantageous. McCann et al. [2] suggest that weak interactions are essential for community persistence.

In Section 2 we compare the mass balance model formulation with related models for a nutrient–prey–predator–omnivore food web. Section 3.1 concerns the competition scenario, in which the omnivore is a specialist and consumes only the prey species. There we derive criteria for coexistence at a non-equilibrium attractor. We analyze the dynamics of the food web when the omnivore is a pure generalist in Section 3.2. The bifurcation diagram resembles that for a food chain where the omnivore consumes the predator only. In that section we describe phenomena due to omnivory, such as a global bifurcation being a heteroclinic connection between a saddle equilibrium at the boundary of the state space and an interior saddle limit cycle. In the Appendix A the numerical technique to calculate the heteroclinic connection is given. In the two-parameter diagram, at one side of the global bifurcation, invasion of the predator in the prey–omnivore system leads to stable coexistence of all trophic levels. On the other side, invasion of the predator leads to extinction of the top-predator. In Section 4 we go into the self-organization of the community composition for a constant environment, in which species are introduced one at the time with the omnivore as last.

2. Description of the models

We start with a description of food web models found in the literature. Table 1 presents the notation. Let $x_0(t)$ denote the density of the non-viable resource (nutrient, substrate). Further, let $x_i(t)$, $i = 1, 2, 3$, denote biomass densities of prey, predator, and omnivore, respectively. When the definition of a parameter involves two trophic levels, two indices are used, separated by a comma. For instance, $\mu_{u,3}$ denotes the maximum growth rate of a omnivore x_3 , feeding on the prey or predator x_u , $u = 1, 2$. Before we introduce the chemostat model, we first discuss some existing related models briefly to explain why we use a different formulation.

Table 1

Parameters and state variables; t = time, m = biomass, v = volume of the reactor

Parameter	Dimension	Units	Interpretation
D	t^{-1}	h^{-1}	Dilution rate
$I_{i-j,i}$	t^{-1}	h^{-1}	Maximum food uptake rate
$k_{i-j,i}$	$m v^{-1}$	$mg dm^{-3}$	Saturation constant
m_i	t^{-1}	h^{-1}	Maintenance rate coefficient
t	t	h	Time
x_0	$m v^{-1}$	$mg dm^{-3}$	Substrate density
x_i	$m v^{-1}$	$mg dm^{-3}$	Biomass density
x_r	$m v^{-1}$	$mg dm^{-3}$	Substrate concentration in reservoir
$\mu_{i-j,i}$	t^{-1}	h^{-1}	Maximum population growth rate

The first index denotes the trophic level, substrate $i = 0$, bacteria $i = 1$, ciliate $i = 2$ and carnivorous ciliate $i = 3$. Some parameters, for instance the saturation constants $k_{i-j,i}$, have double indexes separated by a comma to emphasize that these quantities describe the trophic interactions between two levels.

The Rosenzweig–MacArthur model with omnivory, as used in [2,11], reads

$$\frac{dx_1}{dt} = x_1 \left(r \left(1 - \frac{x_1}{K} \right) - I_{1,2} \frac{x_2}{k_{1,2} + x_1} - \frac{I_{1,3}}{k_{1,3}} \frac{x_3}{1 + x_1/k_{1,3} + x_2/k_{2,3}} \right), \quad (1a)$$

$$\frac{dx_2}{dt} = x_2 \left(\mu_{1,2} \frac{x_1}{k_{1,2} + x_1} - \frac{I_{2,3}}{k_{2,3}} \frac{x_3}{1 + x_1/k_{1,3} + x_2/k_{2,3}} - D_2 \right), \quad (1b)$$

$$\frac{dx_3}{dt} = x_3 \left(\frac{\mu_{1,3}/k_{1,3} x_1 + \mu_{2,3}/k_{2,3} x_2}{1 + x_1/k_{1,3} + x_2/k_{2,3}} - D_3 \right), \quad (1c)$$

where D_i , $i = 2, 3$ is the death rate of the predator and omnivore, respectively. The prey grows logistically with r (intrinsic growth) and K (carrying capacity). The Holling type II functional response describes the interaction between the species.

In the literature a number of mechanistic models are proposed for nutrient uptake modelled following the Holling type II functional response of a predator feeding on a single or multiple prey [21]. Two parameters describe the interaction: the handling time and the search rate. The hyperbolic functional response can be derived using time budgets for these activities. The quotient of the maximum ingestion rate and the saturation constant, I/k is called the attack, catch, search or encounter rate a . The inverse of the saturation constant, $1/k$, is the product of the search rate a and the handling time b . Thus $k = 1/(ab)$ and $I = 1/b$. When a predator feeds on multiple prey species, with different handling time and catch rates, we assume that these prey species are substitutable and individuals from different prey species are caught and handled sequentially at random. When the predator is handling the one prey, it cannot spend time catching the other, so that the one prey species actually benefits indirectly from the abundance of the other.

If $k_{i-1,i} \rightarrow \infty$ and $I_{i-1,i} \rightarrow \infty$, that is $b \rightarrow 0$ while the catch rate $a = I_{i-1,i}/k_{i-1,i}$ remains finite, we have effectively a linear (Lotka–Volterra) functional response. A three species food web including omnivory consisting of resources (mixed bacteria), an intermediate consumer species (ciliate *Tetrahymena*) and an omnivorous species (ciliate *Blepharisma*), is studied by [5] using the Lotka–Volterra

model. Then the ingestion rate of one food source becomes independent of the density of the other.

Conversely, when $k_{i-1,i} \rightarrow 0$ while the ingestion rate $I_{i-1,i}$ and consequently the handling time b is finite, the catch rate goes to infinity, $a \rightarrow \infty$. This effects in a constant scaled functional response equal to 1. That is, the ingestion rate, and therefore also the growth rate, do not depend on the nutrient availability anymore.

To measure the degree of omnivory, McCann et al. [2,11] introduce a parameter ω as $\omega = k_{2,3}/(k_{1,3} + k_{2,3})$ which distinguishes between competition ($\omega = 1, k_{2,3} \rightarrow \infty$) and the tri-trophic food chain ($\omega = 0, k_{1,3} \rightarrow \infty$). In this definition of ω two saturation constants are added and must therefore have the same dimension. In our case an underlying assumption is that the encounter rate is proportional to the prey densities both measured in for instance mg dm^{-3} , see Table 1. In essence ω represents the partition of time the omnivore spends on feeding of the predator and prey. At $\omega = 0.5$ ($k_{1,3} = k_{2,3}$) the omnivore preys on the predator and prey in proportion to their biomass density. Furthermore, in [2,11] an additional parameter is introduced $C_0 = R_{02} = k_{1,3}k_{2,3}/(k_{1,3} + k_{2,3})$. In this paper we use the two parameters $k_{1,3}$ and $k_{2,3}$ themselves to describe the influence of omnivory for reasons that follow.

The lowest level in Eqs. (1a)–(1c) is self-reproducing with logistic growth when predation is absent. This implies hidden assumptions about the nutrient availability. In the mass balance food web models we discuss, non-reproducing nutrients at the base are modelled explicitly. We assume a continuous flow culture with constant influx of nutrients and constant dilution rate for all trophic levels.

In order to be consistent with the nomenclature introduced in earlier papers we call the bottom level the nutrients and the lowest trophic level the prey. The predator and omnivore consume prey, whereas the omnivore also feeds on the predator, see Fig. 1.

The mass balance model for the three species food web, the nutrient–prey–predator–omnivore system, in the chemostat reads

$$\frac{dx_0}{dt} = (x_r - x_0)D - I_{0,1} \frac{x_0}{k_{0,1} + x_0} x_1, \quad (2a)$$

$$\frac{dx_1}{dt} = \left(\mu_{0,1} \frac{x_0}{k_{0,1} + x_0} - \frac{I_{1,3}}{k_{1,3}} \frac{x_3}{1 + x_1/k_{1,3} + x_2/k_{2,3}} - D_1 \right) x_1 - I_{1,2} \frac{x_1}{k_{1,2} + x_1} x_2, \quad (2b)$$

$$\frac{dx_2}{dt} = \left(\mu_{1,2} \frac{x_1}{k_{1,2} + x_1} - \frac{I_{2,3}}{k_{2,3}} \frac{x_3}{1 + x_1/k_{1,3} + x_2/k_{2,3}} - D_2 \right) x_2, \quad (2c)$$

$$\frac{dx_3}{dt} = \left(\frac{\mu_{1,3}/k_{1,3} x_1 + \mu_{2,3}/k_{2,3} x_2}{1 + x_1/k_{1,3} + x_2/k_{2,3}} - D_3 \right) x_3, \quad (2d)$$

where x_r is the concentration substrate in the feed. The depletion rate is the superposition of the dilution rate and the maintenance rate $D_i = D + m_i$. Notice that the model the nutrients at the base of the food web explicitly and this gives the extra ODE (2a) compared to the Rosenzweig–MacArthur model. Hence, the dynamics of the food web in the chemostat with the mass balance model are studied in the positive orthant of $\mathbb{R}_+^4$ compared to $\mathbb{R}_+^3$ for the Rosenzweig–MacArthur model.

Observe that the maximum growth rate of the omnivore consuming the predator and prey equals the maximum of the two maximum growth rates when the predator or prey are consumed separately, thus it equals $\max(\mu_{1,3}, \mu_{2,3})$.

For the sake of simplicity we assume here that the handling time of the omnivore for both of its prey is the same. The search rate for predator and prey individuals may differ, however. Taking the handling times as equal implies that $I_{1,3} = I_{2,3}$. The maximum growth rate $\mu_{1,3}$ is chosen so that the yield $y_{1,3} = y_{1,2}y_{2,3}$. Here we define yield as $y_{u,i} = \mu_{u,i}/I_{u,i}$ where $u = 1, 2$ and $i = 2, 3$ such that $i > u$. The saturation constants $k_{2,3}$ and $k_{1,3}$ will be used as free parameters when the influence of omnivory is to be analyzed. In order to have a well-posed problem we assume that these two parameter are strictly positive.

Model (2) becomes the Marr–Pirt model for a food chain when $k_{1,3} = \infty$. If $k_{1,3} \rightarrow \infty$ the search rate for the omnivore consuming the prey diminishes whereas the handling time, by assumption, remains finite. As a consequence, the omnivore stops to consume the prey and we have effectively a food chain without omnivory. This model has been analyzed in earlier papers [14,15] and its complex dynamic behaviour in [16,17].

Another limiting case is obtained when $k_{2,3} \rightarrow \infty$. Then the omnivore no longer consumes the predator and we have effectively two competitors competing for a single prey which consumes the nutrient. In [19, page 43] the dynamics of a similar system was studied.

This completes the mathematical modelling. We are interested in the asymptotic behaviour of system (2). We will relate the results to those for the two limiting cases, both without omnivory, namely the food chain (omnivore consumes the predator only) and competition between omnivore and predator for prey (omnivore consumes the prey only), see Fig. 1.

3. Bifurcation analysis

Bifurcation analysis gives information about the long-term dynamic behaviour of non-linear dynamic systems. The structural stability is studied with respect to so-called free or bifurcation parameters. For a fixed composition of the species in the food web, the bifurcation parameters are the environmental parameters. In the chemostat case these are the dilution rate, D , and the concentration of nutrients in the feed, x_r , which are under control of the experimenter.

Transcritical bifurcations are important for invasibility. In a supercritical transcritical bifurcation TC^- a stable positive equilibrium or limit cycle originates and in a subcritical version TC^+ an unstable positive equilibrium or limit cycle originates. For supercritical transcritical bifurcation TC^- the invaded species converges to the attractor close to the boundary of the invaded system (the invasion is non-catastrophic). With the subcritical transcritical bifurcation TC^+ there is generally convergence to an attractor far from that of the invaded system (the invasion is catastrophic). Hopf bifurcations mark the origin of limit cycles when a parameter is varied. These limit cycles are stable when the Hopf bifurcation is supercritical H^- and unstable when it is subcritical H^+ .

With application of bifurcation theory to food web models, connections from a non-attracting set on one face of the positive orthant to an attractor on another face or to an attractor in the interior of the positive orthant are important, see also [22,23]. These connections describe invasion in the following way. Suppose that a food web system possesses a positive attractor and that this

attractor is approached, called the non-invaded system and state respectively. Now a species, called the invader, is introduced. The dimension of the system including the invader and its state-space is one greater than that of the non-invaded system. When the non-invaded state is non-attracting with respect to this extended system, the introduced species can invade successfully. The solution of the invaded system will converge to an interior or another boundary attractor in which case another species is doomed to die out. Similarly as in [17] for the food chain case, it can be shown that all orbits starting in the interior of the orthant are bounded also when omnivory is included.

With multiple attractors a separatrix, which is formed by the stable manifold of an unstable invariant set, must exist. Each attractor has a domain of attraction and the invaded system converges to the attractor in whose domain of attraction the non-invaded state lies. When the non-invaded state changes the domain of attraction following upon a variation of a free parameter, we have a global bifurcation. At the bifurcation point there is a heteroclinic connection from the non-invaded state to the unstable invariant set which supports the separatrix. An as-

Table 2

List of all bifurcations, codimension-one curves and codimension-two points

Bifurcation	Description
<i>Codim-1 curves</i>	
$TC_{e,i}^{\pm}$	Transcritical bifurcation: invasion through boundary equilibrium by prey ($i = 1$), predator ($i = 2$) or omnivore ($i = 3$), origin of stable (supercritical, $\pm = -$) or unstable (subcritical, $\pm = +$) interior equilibrium
$TC_{e,32}^{-}$	Transcritical bifurcation: invasion through boundary equilibrium by predator 2 in nutrient–prey–omnivore system, origin of stable interior equilibrium
$TC_{c,3}^{\pm}$	Transcritical bifurcation: invasion through boundary limit cycle omnivore invasion in nutrient–prey–predator system, origin of stable (supercritical, $\pm = -$) or unstable (subcritical, $\pm = +$) interior limit cycle
$TC_{c,32}^{-}$	Transcritical bifurcation: invasion through boundary limit cycle by predator 2 in nutrient–prey–omnivore system, origin of stable interior limit cycle
H_2^{-}	Supercritical Hopf bifurcation for nutrient–prey–predator system food web becomes unstable and origin of stable limit cycle
H_{13}^{-}	Supercritical Hopf bifurcation for nutrient–prey–omnivore food web becomes unstable and origin of stable limit cycle
$H_3^{\pm}$	Hopf bifurcation for nutrient–prey–predator–omnivore system food web becomes unstable and origin of stable (supercritical, $\pm = -$) or unstable (subcritical, $\pm = +$) limit cycle
F_i	Flip bifurcation: period doubling of limit cycle, origin of stable period-2 limit cycle
$Z_{e,2}$	Coexistence of the prey and predator
$G_{e,c}^{\neq}$	Global bifurcation of a heteroclinic connection between equilibrium with $x_2 = 0$ and saddle limit cycle
<i>Codim-2 points</i>	
N	Intersection of $TC_{e,2}$, $TC_{e,13}$
M_1	Intersection of H_2^{-} , $TC_{e,3}$, $TC_{c,3}$
M_2	Intersection of $TC_{e,3}$, $T_{e,3}$
M_3	Intersection of $TC_{c,3}$, $T_{c,3}$
M_4	Intersection of H_{13}^{-} , $TC_{e,32}$, $TC_{c,32}$
P_1, P_2	Intersection of $TC_{e,32}$, F_{13} , F_3
G	Intersection of $TC_{c,3}$, $TC_{e,13}$, $G_{e,c}^{\neq}$

sembly sequence from bare space to a field inhabited by all species, is formed when species are introduced one at a time, and after the invaded system approached an attractor. This goes on until the end-point is resistant to further invasion. Note that the connections to the end-point are not heteroclinic connections because it terminates at an attractor, but in previous stages of the sequence they are.

Table 2 lists the important bifurcation curves and points. The local bifurcation curves are calculated with *LOCBIF*: [24,25] and *AUTO*: [26]. The global bifurcation is continued with the numerical technique described in the Appendix A.

The values of the vital parameters of the populations and of those describing the population interaction are given in Table 4 and are based on measured data given in [12] for a microbial food chain.

In the following sections we start in Section 3.1 with the description of dynamic behaviour of the predator–omnivore competition model and continue in Section 3.2 with the numerical bifurcation analysis of a model with the generalist omnivore where it consumes the predator and prey proportional to their biomass.

3.1. Predator–omnivore competition, $k_{1,3} = 1$ and $k_{2,3} = \infty$

First, we consider the dynamics of the two bi-trophic food chains nutrient–prey–predator and nutrient–prey–omnivore separately. Fig. 2 depicts both the bifurcation diagrams for these two bi-trophic food chain, calculated with the system (2) where $x_2 = 0$ or $x_3 = 0$ in one figure. The

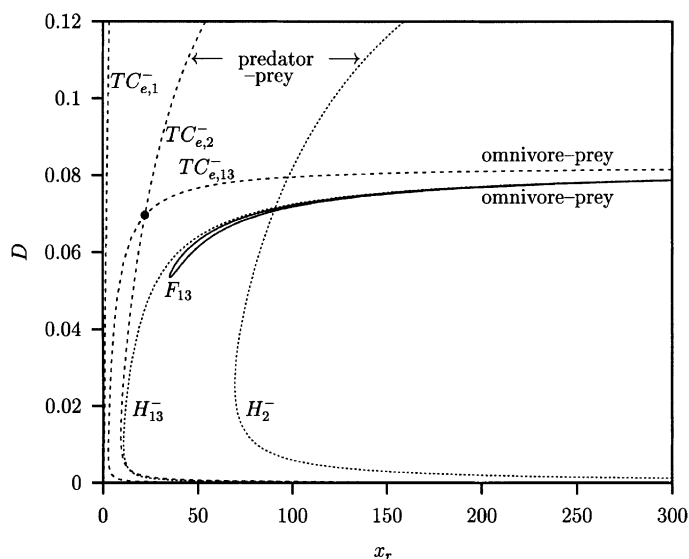


Fig. 2. Superposition of two bifurcation diagrams for model (2) with $x_2 = 0$ (omnivore–prey) and $x_3 = 0$ (predator–prey). The bifurcation parameters are the dilution rate D and the substrate concentration in reservoir x_r . Values assigned to physiological parameters are listed in Table 4. The curve $TC_{e,1}^-$ marks supercritical transcritical bifurcation where the prey x_1 invades and is the same for both cases. The curves $TC_{e,2}^-$, $TC_{e,13}^-$ are transcritical bifurcation curves, and H_2^- and H_{13}^- mark supercritical Hopf bifurcation curves for the predator–prey, $x_3 = 0$ and the omnivore–prey bi-trophic food chain, $x_2 = 0$, respectively.

Table 3

Equilibria and limit cycles of the nutrient–prey–predator–omnivore food web (Fig. 1). The bar denotes the equilibrium value of the state variable and the tilde their periodic fluctuations in the limit cycles case

	Equilibrium	Limit cycle	Complex
Nutrient	$E_0 = (\bar{x}_0, 0, 0, 0)$		
Nutrient–prey	$E_1 = (\bar{x}_0, \bar{x}_1, 0, 0)$		
Nutrient–prey–predator	$E_2 = (\bar{x}_0, \bar{x}_1, \bar{x}_2, 0)$	$L_2 = (\tilde{x}_0, \tilde{x}_1, \tilde{x}_2, 0)$	
Nutrient–prey–omnivore	$E_{13} = (\bar{x}_0, \bar{x}_1, 0, \bar{x}_3)$	$L_{13} = (\tilde{x}_0, \tilde{x}_1, 0, \tilde{x}_3)$	C_{13}
Nutrient–prey–predator–omnivore	$E_3 = (\bar{x}_0, \bar{x}_1, \bar{x}_2, \bar{x}_3)$	$L_3 = (\tilde{x}_0, \tilde{x}_1, \tilde{x}_2, \tilde{x}_3)$	C_3

parameter values are given in Table 1, except $k_{1,3} = 1$. The curves $TC_{e,1}^-$, $TC_{e,2}^-$ and $TC_{e,13}^-$ are transcritical bifurcation curves and H_2^- and H_{13}^- mark supercritical Hopf bifurcation curves. With fixed dilution rate D (for example $D = 0.02$) and increasing x_r , that is enrichment, the sequence of attractors for the nutrient–prey–predator system is

$$E_0 \xrightarrow{TC_{e,1}^-} E_1 \xrightarrow{TC_{e,2}^-} E_2 \xrightarrow{H_2^-} L_2. \quad (3)$$

We use the notation introduced in Table 3. The bifurcation curves $TC_{e,1}^-$, $TC_{e,2}^-$ and H_2^- are the only bifurcation curves found in the region of the bifurcation diagram we investigate. This is an example of a simple sequence. First, when no species is present there is the stable equilibrium E_0 , $\bar{x}_0 = x_r$. When the prey is introduced at a higher x_r level, this equilibrium is unstable in $\mathbb{R}_+^2$ and there is convergence to the stable equilibrium $E_1 \in \text{int} \mathbb{R}_+^2$. When the predator is introduced and x_r is increased further there is a stable equilibrium $E_2 \in \text{int} \mathbb{R}_+^3$. When the x_r is increased even further the system approaches a stable limit cycle $L_2 \in \text{int} \mathbb{R}_+^3$ and this is associated with the ‘paradox of enrichment’.

For the nutrient–prey–omnivore system this sequence of attractors is

$$E_0 \xrightarrow{TC_{e,1}^-} E_1 \xrightarrow{TC_{e,13}^-} E_{13} \xrightarrow{H_{13}^-} L_{13}. \quad (4)$$

For this nutrient–prey–omnivore food chain the curve F_{13} marks a flip bifurcation. Calculations revealed that this flip bifurcation forms the starting point of a cascade of period doubling bifurcations leading to chaos. Notice that without maintenance ($m_i = 0$ or $D_i = D$ for $i = 1, 2, 3$) chaos is impossible because the system can be reduced to a two dimensional system when asymptotic behaviour is concerned and the conservation principle described in [19] is used.

Now, the predator and omnivore compete for the prey in the chemostat. In this case, the omnivore is a specialist where it consumes the prey but not the predator, that is $k_{2,3} \rightarrow \infty$. The equations read

$$\frac{dx_0}{dt} = (x_r - x_0)D - I_{0,1}f_{0,1}x_1, \quad (5a)$$

$$\frac{dx_1}{dt} = (\mu_{0,1}f_{0,1} - D_1)x_1 - I_{1,2}f_{1,2}x_2 - I_{1,3}f_{1,3}x_3, \quad (5b)$$

$$\frac{dx_2}{dt} = (\mu_{1,2}f_{1,2} - D_2)x_2, \quad (5c)$$

Table 4

Parameter set for bacterium-ciliate models, after [12,13]

Parameter	Unit	Values			
		$i = 1$	$i = 2$	$i = 3$	
		$j = 1$	$j = 1$	$j = 1$	$j = 2$
$\mu_{i-j,i}$	h^{-1}	0.5	0.2	0.15	0.09
$k_{i-j,i}$	mg dm^{-3}	8	9	10	10
$I_{i-j,i}$	h^{-1}	1.25	0.33	0.25	0.25
m_i	h^{-1}	0.025	0.01	0.0075	

The values for the maintenance rate coefficients are taken 5% of the maximum growth rate. The ranges for the control parameters are $0 < D < \mu_{0,1}$ and $0 < x_r \leq 300 \text{ mg dm}^{-3}$. Notice that we took for the yield $y_{1,3} = \mu_{1,3}/I_{1,3} = y_{1,2}y_{2,3} = 0.36$ and consequently we have $\mu_{1,3} = 0.6\mu_{2,3}$ since we assumed $I_{1,3} = I_{2,3}$. The values are for a generalist omnivore.

$$\frac{dx_3}{dt} = (\mu_{1,3}f_{1,3} - D_3)x_3, \quad (5d)$$

where we use the (scaled) Holling type II functional response denoted by $f_{u,i}$ and defined by

$$f_{u,i} = \frac{x_u}{k_{u,i} + x_u}. \quad (6)$$

Let $\mathcal{M}_{1,i}(x_1)$, for $i = 2, 3$, denote the actual specific growth rate of population x_i consuming their prey x_1 defined as

$$\mathcal{M}_{1,i}(x_1) = \left(\mu_{1,i} \frac{x_1}{k_{1,i} + x_1} - m_i \right). \quad (7)$$

Let the dilution rate denoted by D^* be determined by the condition that the growth rate for the two competitors is the same. It forms together with the nutrient concentration $\bar{x}_1^*$, where the bar denotes the equilibrium value, the solution of the following two equations:

$$\mathcal{M}_{1,2}^* \stackrel{\text{def}}{=} \mu_{1,2} \frac{\bar{x}_1^*}{k_{1,2} + \bar{x}_1^*} - m_2 = D^*, \quad (8a)$$

$$\mathcal{M}_{1,3}^* \stackrel{\text{def}}{=} \mu_{1,3} \frac{\bar{x}_1^*}{k_{1,3} + \bar{x}_1^*} - m_3 = D^*. \quad (8b)$$

With the values given in Table 4 where $k_{1,3} = 1$ instead of $k_{1,3} = 10$ the critical value for the dilution rate is $D^* = 0.06953$. This implies that the two transcritical curves for the competing predator and omnivore $TC_{e,2}^-$ and $TC_{e,13}^-$, respectively, intersect in the point denoted by N where $D = D^*$.

Fig. 3 depicts the two-parameter bifurcation diagram where the dilution rate D and the concentration in the feed x_r are the free parameters. On the curve $Z_{e,2}$ both predators can coexistence in equilibrium with the prey. The solution is, however, degenerated that is the solutions of the equilibrium equations form a one-dimensional manifold in the state space fixed by a linear relationship between x_2 and x_3 . Between N and M_4 the other three eigenvalues have negative real part for positive biomasses x_2 and x_3 . On the right-hand side of point M_4 (also of point M_1) two eigenvalues have negative real parts.

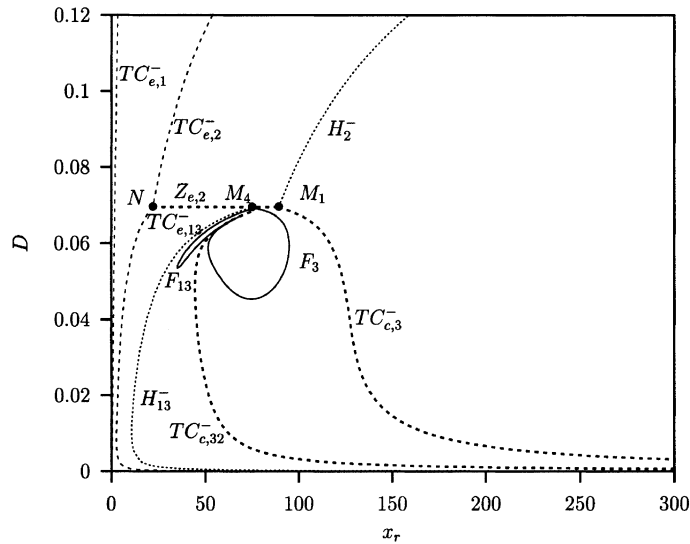


Fig. 3. Bifurcation diagram for model with pure competition between the omnivore and the predator system (5). The bifurcation parameters are the dilution rate D and the substrate concentration in reservoir x_r . Values assigned to physiological parameters are listed in Table 4 where $k_{1,3} = 1$ and $k_{2,3} = \infty$. The curves $TC_{e,1}^-$, $TC_{e,2}^-$, $TC_{e,13}^-$, $TC_{c,32}^-$, $TC_{c,3}^-$ are transcritical bifurcation curves for equilibria, $TC_{c,32}^-$, $TC_{c,3}^-$ for limit cycles, and H_2^- and H_{13}^- mark supercritical Hopf bifurcation curves for the bi-trophic food chains without omnivore, $x_3 = 0$ and predator, $x_2 = 0$, respectively.

In [19, page 43] also competition at a higher trophic level is dealt with. However, the growth rates are of the Monod type, that is no maintenance is assumed: $m_i = 0$ or $D_i = D$ for all i . It is proven that the two predators x_2 and x_3 could survive on a common prey x_1 and conditions for the parameters are derived. Furthermore it is mentioned that chaotic behaviour was observed.

Fig. 3 shows the calculated transcritical curves for limit cycles $TC_{c,3}^-$ originating in codim-2 point M_1 , and curve $TC_{c,32}^-$ originating in M_4 . Crossing the $TC_{c,3}^-$ curve inward into the region between the two curves the omnivore can invaded the cycling nutrient–prey–predator system and crossing the curve $TC_{c,32}^-$ the predator can invaded the cycling nutrient–prey–omnivore system. In agreement with the results presented in [19, page 43] there is coexistence of the two predator populations as a non-equilibrium attractor between the curves $TC_{c,3}^-$ and $TC_{c,32}^-$.

In [17] we discussed the link between invasion and the transcritical bifurcation. The growth rate of the omnivore $\mathcal{M}_{1,3}$ is proportional to its biomass x_3 and this implies directly that the invasion criterion equals $\mathcal{M}_{1,3} > D$ for equilibrium $E_2 = (\bar{x}_0, \bar{x}_1, \bar{x}_2, 0)$ and for a limit cycle $L_2 = (\tilde{x}_0, \tilde{x}_1, \tilde{x}_2, 0)$ it is $T_0^{-1} \int_0^{T_0} \mathcal{M}_{1,3}(t) dt > D$ where T_0 is the period, see [17,19]. When the equal sign holds, these two criteria are equivalent with the requirement that one eigenvalue equals zero at the equilibrium and one Floquet multiplier has magnitude equal to one at the limit cycle and this fixes the transcritical bifurcation.

The curve marked by F_3 denotes a flip bifurcation. Inside the region bounded by the curve F_3 a cascade of period doubling leads to chaotic behaviour, but we will not explore this further. The situation close to the codim-2 point M_4 is more complicated. Fig. 4 shows a detail of the bifurcation diagram around the codim-2 point M_4 . In two additional codim-2 points P_1 and P_2 the flip bifurcation curve F_3 intersects the transcritical bifurcation curve $TC_{c,32}^-$. In these points one

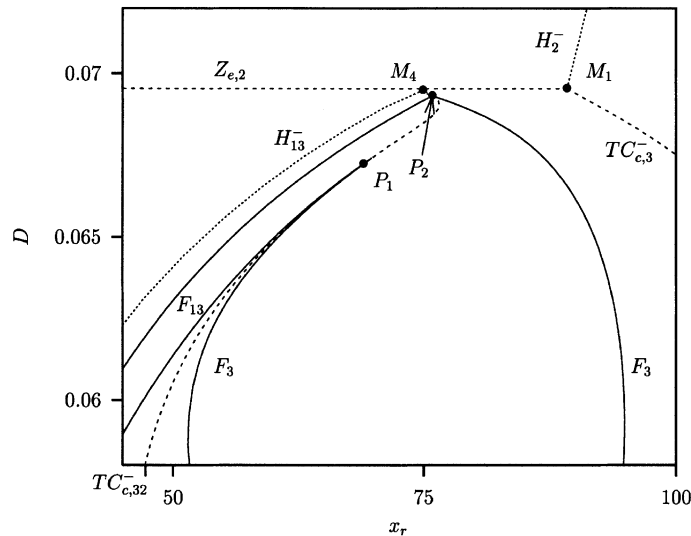


Fig. 4. Detail of Fig. 3. In the codimension-two bifurcation points, P_j , $j = 1, 2$ the flip bifurcation curves F_{13} and F_3 intersect each other and the transcritical curve $TC_{c,32}^-$.

Floquet multiplier equals -1 because of the flip bifurcation, F_3 , and one equals 1 because of the transcritical bifurcation, $TC_{c,32}^-$. There are four multipliers for this four dimensional nutrient–prey–predator–omnivore system, and since one multiplier equals always 1 for the motion along the orbit, there is one multiplier not on the unit circle in the complex plane. The magnitude of this multiplier was less than 1 for the parameter values given in Table 4 where $k_{1,3} = 1$. Furthermore, because these points are on the transcritical bifurcation curves $TC_{c,32}^-$ we have $x_2 = 0$ and this implies that points P_1 and P_2 are also on the flip bifurcation curve F_{13} for the three dimensional nutrient–prey–omnivore system.

Fig. 5 explains what happens when the curve between the two points N and M_1 is crossed by varying D . Between N and M_4 the curve $Z_{e,2}$ coincides actually with both bifurcation curves $TC_{e,13}^-$ and $TC_{e,3}^-$ and between M_4 and M_1 with the two bifurcation curves H_3^- and $TC_{e,3}^-$. When $D > D^*$ in the neighbourhood of $Z_{e,2}$ the predator always out-competes the omnivore and there is a stable equilibrium E_2 , that is $x_2 > 0$ and $x_3 = 0$. No non-equilibrium attractor exists in this region of the bifurcation diagram and therefore classical competitive exclusion holds true. For $D < D^*$ in the neighbourhood of $Z_{e,2}$ between the points N and M_4 , the omnivore always out-competes the predator, that is $x_2 = 0$ and $x_3 > 0$. However, just below the $Z_{e,2}$ curve and between the points M_1 and M_4 , there is coexistence as a non-equilibrium attractor: a limit cycle L_3 .

3.2. The generalist omnivore, $k_{1,3} = 10$, $k_{2,3} = 10$

In this section we discuss the bifurcation diagram displayed in Fig. 6 for the whole food web including the omnivore which is now a generalist, $k_{1,3} = 10$ and $k_{2,3} = 10$. Besides the handling time by the omnivore, also the search rate is the same for both predator and prey individuals. The

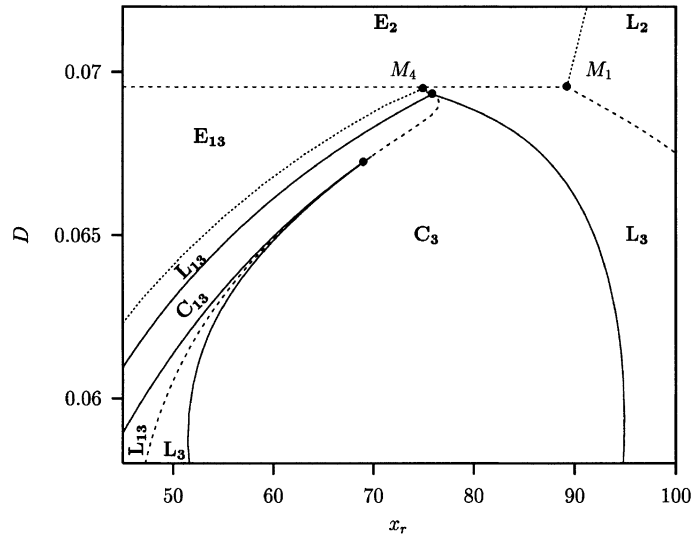


Fig. 5. Detail of Fig. 3 where only the codimension-two bifurcation points and the attractor types defined in Table 3 are indicated.

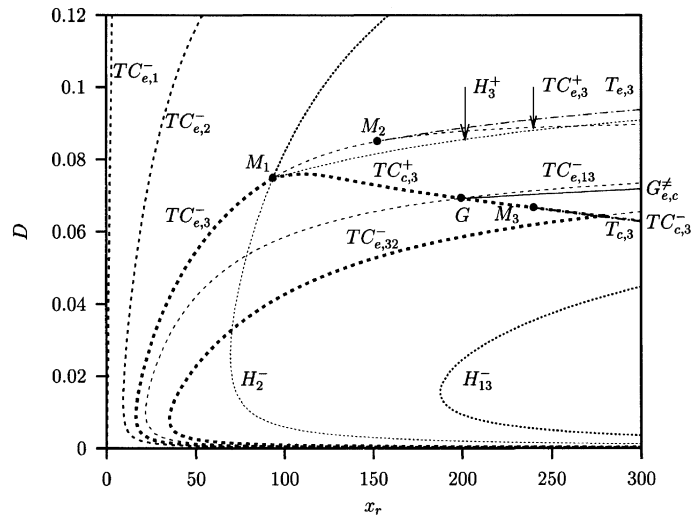


Fig. 6. Bifurcation diagram for the model with omnivory: system (2). The bifurcation parameters are the dilution rate D and the substrate concentration in reservoir x_r . Values assigned to physiological parameters are listed in Table 4 where $k_{1,3} = 10$ and $k_{2,3} = 10$. The curves $TC_{e,1}^-$, $TC_{e,2}^-$, $TC_{e,32}^-$, $TC_{e,3}^-$ are transcritical bifurcation curves for equilibria, $TC_{c,3}^+$ for limit cycles and H_2^- , H_{13}^- mark supercritical Hopf bifurcation curves all for the bi-trophic food chains without and with perturbations of the vital rates. The curve H_3^+ marks a subcritical Hopf bifurcation for the complete food web. Point G is a codimension two point for a global bifurcation where the global bifurcation curve $G_{e,c}^\neq$ originates.

omnivore preys on the predator and prey in proportion to their biomass density. For the growth rate of the omnivore the two terms are weighted by the maximum growth rates on the predator $\mu_{2,3}$ and prey $\mu_{1,3}$ separately.

The diagram Fig. 6 shows the calculated transcritical curves for equilibria $TC_{e,3}^-$ originating in codim-2 point M_1 and curve $TC_{e,32}^-$ originating in M_4 besides the curves already discussed in the previous subsection.

Let the specific growth rate of the predator, $\mathcal{M}_2$, be defined as

$$\mathcal{M}_2 = \mu_{1,2} \frac{x_1}{k_{1,2} + x_1} - \frac{I_{2,3}}{k_{2,3}} \frac{x_3}{1 + x_1/k_{1,3} + x_2/k_{2,3}} - m_2. \quad (9)$$

In an equilibrium $E_{13} = (\bar{x}_0, \bar{x}_1, 0, \bar{x}_3)$ the invasion criterion reads $\mathcal{M}_2 > D$ where the growth rate is calculated in the equilibrium. When invasion is via a limit cycle $L_{13} = (\tilde{x}_0, \tilde{x}_1, 0, \tilde{x}_3)$ the criterion reads $T_0^{-1} \int_0^{T_0} \mathcal{M}_2(t) dt > D$, where T_0 is again the period.

Note that the specific growth rate of the invading species, in this case the predator, into the virgin environment depends on the abundance of its prey, but also on that of the rival, in this case the omnivore. More prey is advantageous now for two reasons, directly from the first term of the right-hand side of Eq. (9) but also indirectly from the second term, because the omnivore spends also time on handling the prey and this diminishes the rate at which it is consumed by the omnivore.

Similar invasion criteria hold for the invasion of the omnivore in the nutrient–prey–predator system where the specific growth rate of the omnivore $\mathcal{M}_3$ is defined as

$$\mathcal{M}_3 = \frac{\mu_{1,3}/k_{1,3} x_1 + \mu_{2,3}/k_{2,3} x_2}{1 + x_1/k_{1,3} + x_2/k_{2,3}} - m_3. \quad (10)$$

In Fig. 7 the omnivore invades the predator–prey system via a limit cycle $L_2 = (\tilde{x}_0, \tilde{x}_1, \tilde{x}_2, 0)$ because $T_0^{-1} \int_0^{T_0} \mathcal{M}_3(t) dt > D$ where the growth rate $\mathcal{M}_3(t)$ is integrated along the limit cycle. The system converges to three different end-points depending on the environmental conditions D and x_r .

The diagram depicted in Fig. 6 resembles that of a food chain, already shown and discussed in [15]. Here we discuss only phenomena due to omnivory. In a food chain a species at a higher trophic level can only exist when species at all lower trophic levels exist. This does not hold true for omnivory, the omnivore at level three can exist without the predator at level two since it can live on prey only. This gives the ‘new’ transcritical bifurcation curves TC_{13}^- and TC_{32}^- . It is possible that, for instance, the predator establishes itself while the omnivore is eliminated or the other way around. Furthermore, the end-point of the food web depends on the order in which the predator and the omnivore are introduced.

In Fig. 8 the equilibrium values for the biomass $\bar{x}_1$, $\bar{x}_2$ and $\bar{x}_3$ are displayed for various dilution rates $0.06 \leq D \leq 0.1$ where $x_r = 300$. The long-term extreme values for $\tilde{x}_3$ are shown where the attracting state is a limit cycle.

The arrows in Fig. 8 indicate a hysteresis loop. Following the positive solid curves in the direction of the arrow we find stable equilibria at increasing dilution rates. Then suddenly the system collapses. The downward arrow indicates that the omnivore is doomed to die out. The system becomes a stable oscillating bi-trophic food chain, as indicated by the solid line at $x_3 = 0$, and invasion by the omnivore is impossible. The omnivore can invade the nutrient–prey–predator system when the dilution rate is lowered sufficiently. Following the arrow to the left, the bi-trophic limit cycle becomes unstable. When a small amount of omnivore is introduced to the system at lower dilution rates, the system evolves to a stable limit cycle of the nutrient–prey–predator–omnivore system in a small range for the dilution rate. For D values below this point, invasion of

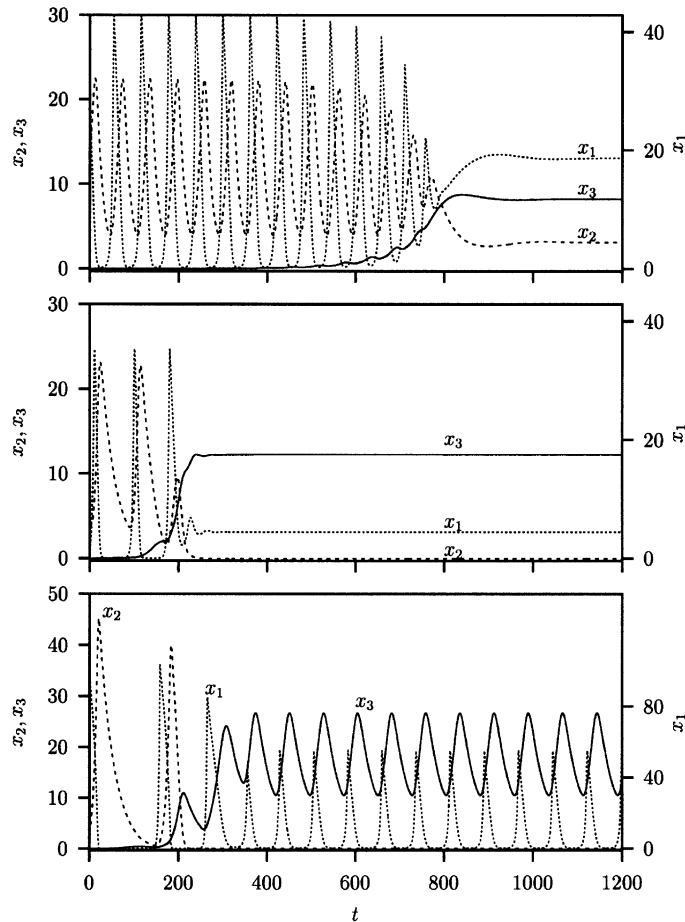


Fig. 7. Invasion of the omnivore. Time evolution for the biomass densities x_1 , x_2 and x_3 are shown. At $t = 0$ the omnivore is inoculated at a small value close to the saddle limit cycle L_2 , and the omnivore invades the system. For parameters values $D = 0.06$ and $x_r = 150$ (top) the system converges to the positive stable equilibrium E_3 ($L_2 \rightarrow E_3$), for $D = 0.02$ and $x_r = 150$ (middle) to the stable equilibrium E_{13} where $x_2 = 0$ ($L_2 \rightarrow E_{13}$) and $D = 0.02$ and $x_r = 300$ (bottom) to the stable limit cycle L_{13} ($L_2 \rightarrow L_{13}$).

the nutrient–prey–predator system is possible. Initially the system cycles in the $x_3 = 0$ subspace. When the omnivore is inoculated the solution approaches an equilibrium where the predator is absent, similar as in the middle panel of Fig. 7. Hence the omnivore stabilizes the cycling system and it replaces the predator, a form of competitive exclusion again.

The sharp bend in the equilibrium values of the biomasses found when D is increased again, marks the point above which persistence of all populations is possible. Finally, when the dilution rate is increased further, the system remains stable until the omnivore gets suddenly washed-out again.

These phenomena are now explained using the one-parameter bifurcation diagram depicted in Fig. 9. We follow the same loop and the transitions are now indicated by the types of bifurcation that occur. For D values above the subcritical Hopf bifurcation H_3^+ the omnivore is washed-out.

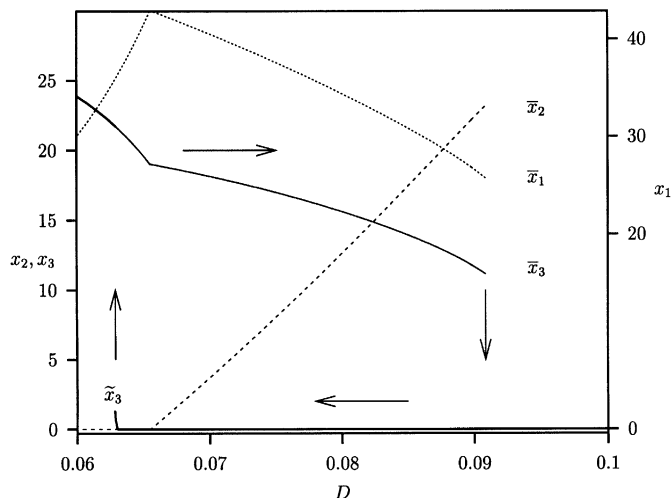


Fig. 8. The attracting solution values for the prey, x_1 , the predator, x_2 , and the generalist omnivore, x_3 and its extreme values $\tilde{x}_3$. The arrows indicate a hysteresis loop. The varying parameter is the dilution rate D . The concentration in the reservoir equals $x_r = 300$. Values assigned to physiological parameters are listed in Table 4.

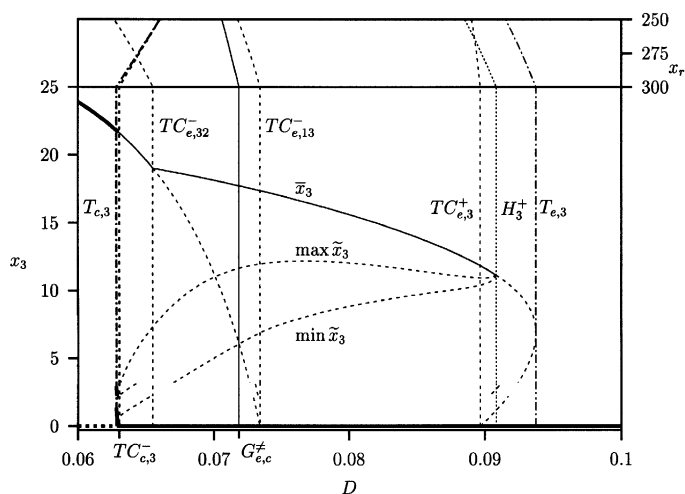


Fig. 9. One-parameter bifurcation diagram with equilibrium values of the predator x_2 and omnivore x_3 and the extreme values of the omnivore $\tilde{x}_3$ for the generalist omnivore where $k_{1,3} = 10$ and $k_{2,3} = 10$. Solid curves give stable equilibrium values and extreme values of stable limit cycles. Dashed curves give unstable equilibrium and extreme values. At the top the rotated two-parameter bifurcation diagram, Fig. 6 is plotted for $250 \leq x_r \leq 300$. The curve $G_{e,c}^\#$ is the heteroclinic connection between E_{13} and L_3 .

At the Hopf bifurcation point an unstable limit cycle originates for decreasing D . This limit cycle supports a separatrix between the interior equilibrium attractor and the boundary limit cycle with $x_3 = 0$. This shows that invasion is impossible for D values between the curves H_3^+ and $TC_{c,3}^-$. Below $TC_{c,3}^-$ invasion is possible and the attractor is a stable limit cycle. This stable limit cycle becomes unstable at the tangent bifurcation point $T_{c,3}$. Thus below $T_{c,3}$ invasion from the

boundary limit cycle is catastrophic with convergence to the stable equilibrium without predators. Between the two bifurcations $T_{c,3}$ and $TC_{c,32}^-$ a stable limit cycle for the complete food web coexists with a stable equilibrium where the predator is absent, $x_2 = 0$. The saddle limit cycle in between acts again as a separatrix. At the transcritical bifurcation point $TC_{c,32}^-$ the predator appears and there is a stable equilibrium for the nutrient–prey–predator–omnivore system for D values above this point. This gives the sharp bend in the equilibrium values for the omnivore at that point. For increasing D the system remains positive and stable until the catastrophic bifurcation H_3^+ .

The curve $TC_{c,13}^-$ marks the D value above which the omnivore can invade the nutrient–prey system. As explained in the next paragraph, since $k_{2,3} = 10$, with pure competition of the predator and omnivore both consuming the prey, the predator wins for all D values.

There must be a global bifurcation for the heteroclinic connection of the boundary saddle equilibrium $E_{1,3}$ to the interior saddle limit cycle L_3 which originates at the subcritical Hopf bifurcation H_3^+ . Between the two curves $TC_{c,3}^-$ and $TC_{e,13}^-$ there are two attractors, the stable equilibrium point E_3 and the limit cycle L_2 which is also stable because invasion via the omnivore is impossible for D values between $TC_{c,3}^-$ and $TC_{e,13}^-$. Since the equilibrium $E_{1,3}$ is unstable, intro-

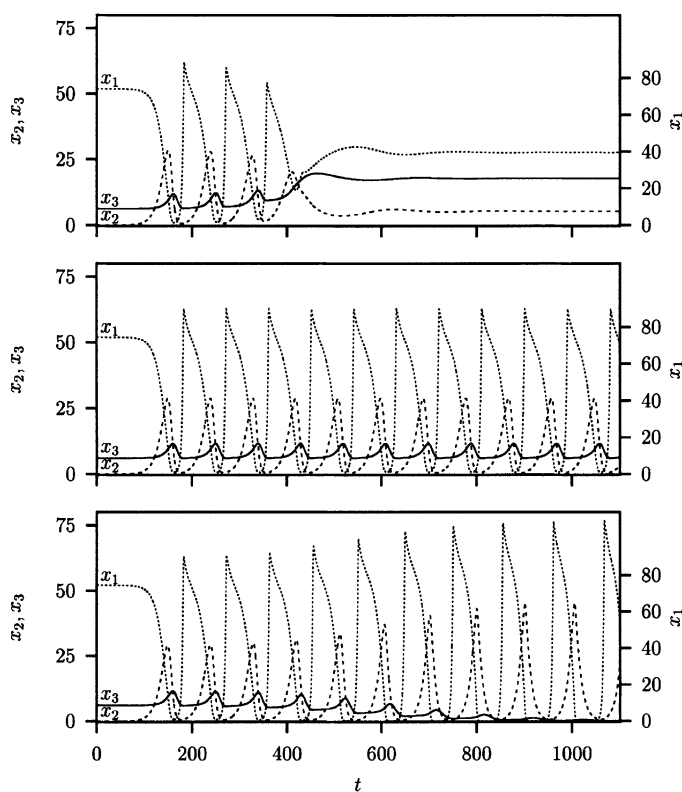


Fig. 10. Invasion of the predator near a heteroclinic bifurcation. Time evolution for the biomass densities x_1 , x_2 and x_3 are shown. The parameters values are as in Fig. 8. At $t = 0$ the predator is inoculated at a small value close to the saddle equilibrium $E_{1,3}$ and the predator invades the system. For $D = 0.0718$ (top) the system converges to the positive stable equilibrium E_3 ($E_{1,3} \rightarrow E_3$) while for $D = 0.07185$ (bottom) to the stable limit cycle L_2 where $x_3 = 0$ ($E_{1,3} \rightarrow L_2$). For $D = 0.07183$ (middle) the heteroclinic connection between $E_{1,3}$ and L_3 which supports the separatrix is plotted ($E_{1,3} \rightarrow L_3$).

duction of the predator leads to invasion, but it is not clear to which attractor the system will evolve. It converges to the attractor in the basin of attraction of which it lies. The separatrix between these attractors is the stable manifold of the saddle limit cycle L_3 . Thus when the saddle equilibrium $E_{1,3}$ lies on this manifold, the system converges to the unstable limit cycle. When D is below the global bifurcation point we are looking for, invasion of the predator via $E_{1,3}$ leads to convergence to the interior stable equilibrium point E_3 similar to the case at point $TC_{e,32}^-$ and when above that point to the stable limit cycle L_2 similar to the case at point $TC_{e,13}^-$ where the omnivore goes extinct. In the latter case the invading predator replaces the omnivore and this is just the reverse case when D is smaller than $TC_{e,3}^-$ where the omnivore replaces the predator. This heteroclinic connection is indicated by $G_{e,c}^\#$ in Fig. 9 and marks a global bifurcation. In Fig. 10 the solutions for three D -values and $x_r = 300$ are shown. In the top panel the dilution rate is slightly smaller than for $G_{e,c}^\#$ and the invaded system converges to the interior equilibrium E_3 , that is there is a connection from E_{13} to E_3 . There is convergence to the boundary limit cycle where $x_3 \downarrow 0$ when D is just above the value for $G_{e,c}^\#$. This is a connection between E_{13} and L_2 . The middle panel shows the heteroclinic connection to the interior saddle limit cycle L_3 . Thus, the curve $G_{e,c}^\#$ gives the additional information to which of the two attractors the system will converge after invasion, while the transcritical bifurcations determine whether or not invasion is possible.

The heteroclinic bifurcation $G_{e,c}^\#$ originates at point G , shown in two-parameter diagram Fig. 6, where the heteroclinic connection between E_{13} and L_3 enters the positive orthant through the boundary $x_3 = 0$. Since the hyperplane $x_3 = 0$ is invariant, this means that at point G there must be transcritical bifurcations for E_{13} and L_3 . It follows that point G is the crossing point between $TC_{e,13}^-$ and $TC_{e,3}^+$. In the Appendix A the algorithm for the calculation of the heteroclinic connection and its continuation in the two-parameter plane is described.

4. Consequences of omnivory

In this section we change the two parameters $k_{1,3}$ and $k_{2,3}$ which fix in our approach the strength of omnivory. We will study invasion of the omnivore in an existing predator–prey system. Consequently the end-points are reached via a unique sequence of connections, depending on the environmental conditions D and x_r :

$$\begin{array}{ccccccc}
 \mathbb{R}_+^1 & & \mathbb{R}_+^2 & & \mathbb{R}_+^3 & & \mathbb{R}_+^4 \\
 & & & & \nearrow & & E_3 \\
 E_0 & \rightarrow & E_1 & \rightarrow & E_2 & \rightarrow & L_3 \\
 & & & & \searrow & & \\
 & & & & \nearrow & & E_3 \\
 & & & & L_2 & \rightarrow & L_3 \\
 & & & & \searrow & & C_3
 \end{array} \tag{11}$$

For a number of representative values we present the two-parameter bifurcation diagrams in Figs. 11 and 12. In these diagrams the codim-2 points are shown together with the end-points of the assembly where we use the notation introduced in Table 3.

In the diagrams in Figs. 11 and 12 the regions where the end-points are in the interior of $\mathbb{R}_+^4$, are indicated in grey inside the thick dotted lines. The end-points are the positive equilibrium, E_3 , a periodic orbit, L_3 , or a chaotic attractor, C_3 .

First, we discuss the diagrams depicted in Fig. 11 where both parameters $k_{1,3}$ and $k_{2,3}$ were altered simultaneously. In the first column the saturation parameter $k_{1,3} = 1$ and in the second $k_{1,3} = 10$. The other saturation parameter $k_{2,3}$ has three values $k_{2,3} = \infty, 10, 1$.

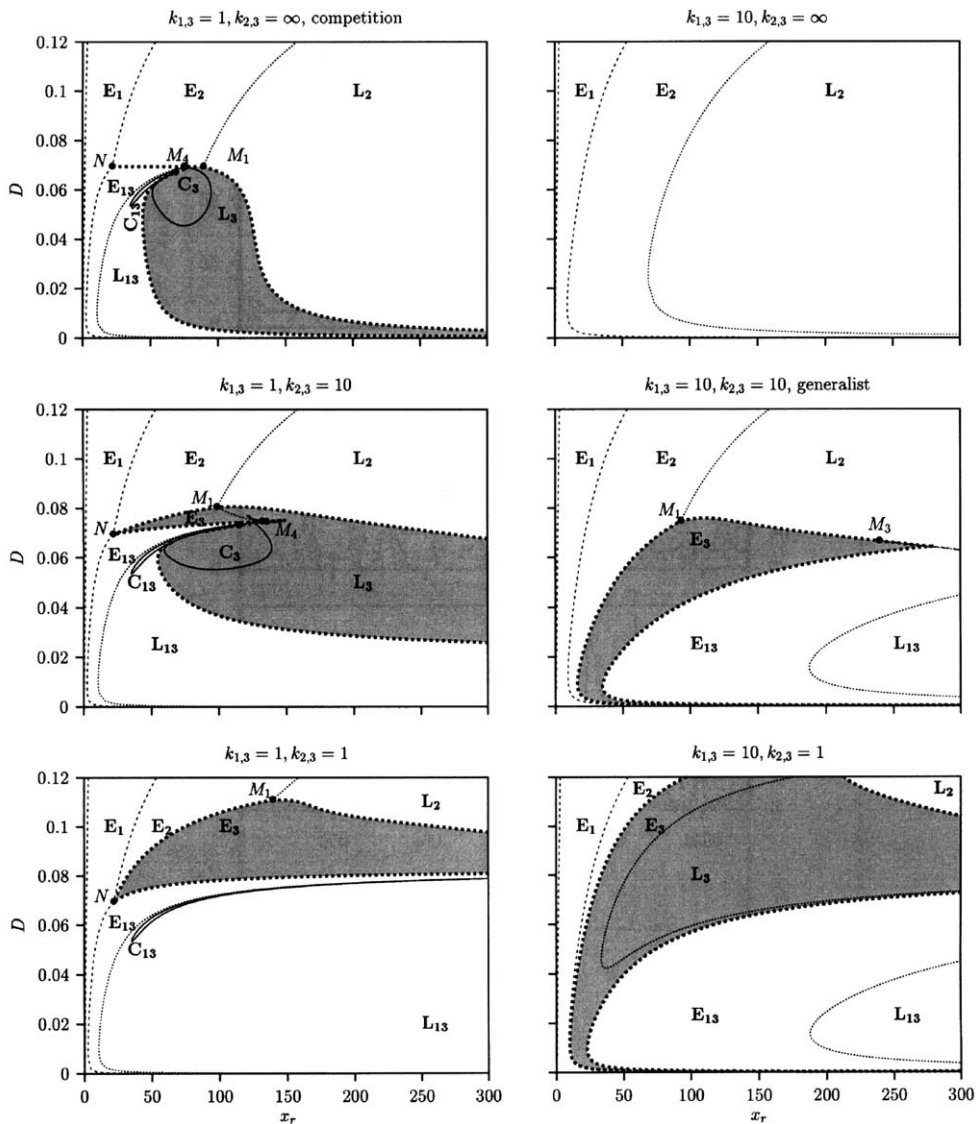


Fig. 11. Bifurcation diagrams where both parameters $k_{1,3}$ and $k_{2,3}$ for the omnivore–prey and omnivore–predator trophic interaction are varied. Left column with $k_{1,3} = 1 < k_{1,3}^*$, see (13), and right column with $k_{1,3} = 10 > k_{1,3}^*$, where $k_{2,3} = \infty, k_{2,3} = 10$ and $k_{2,3} = 1$ from top to bottom. The gray regions mark coexistence of the three species.

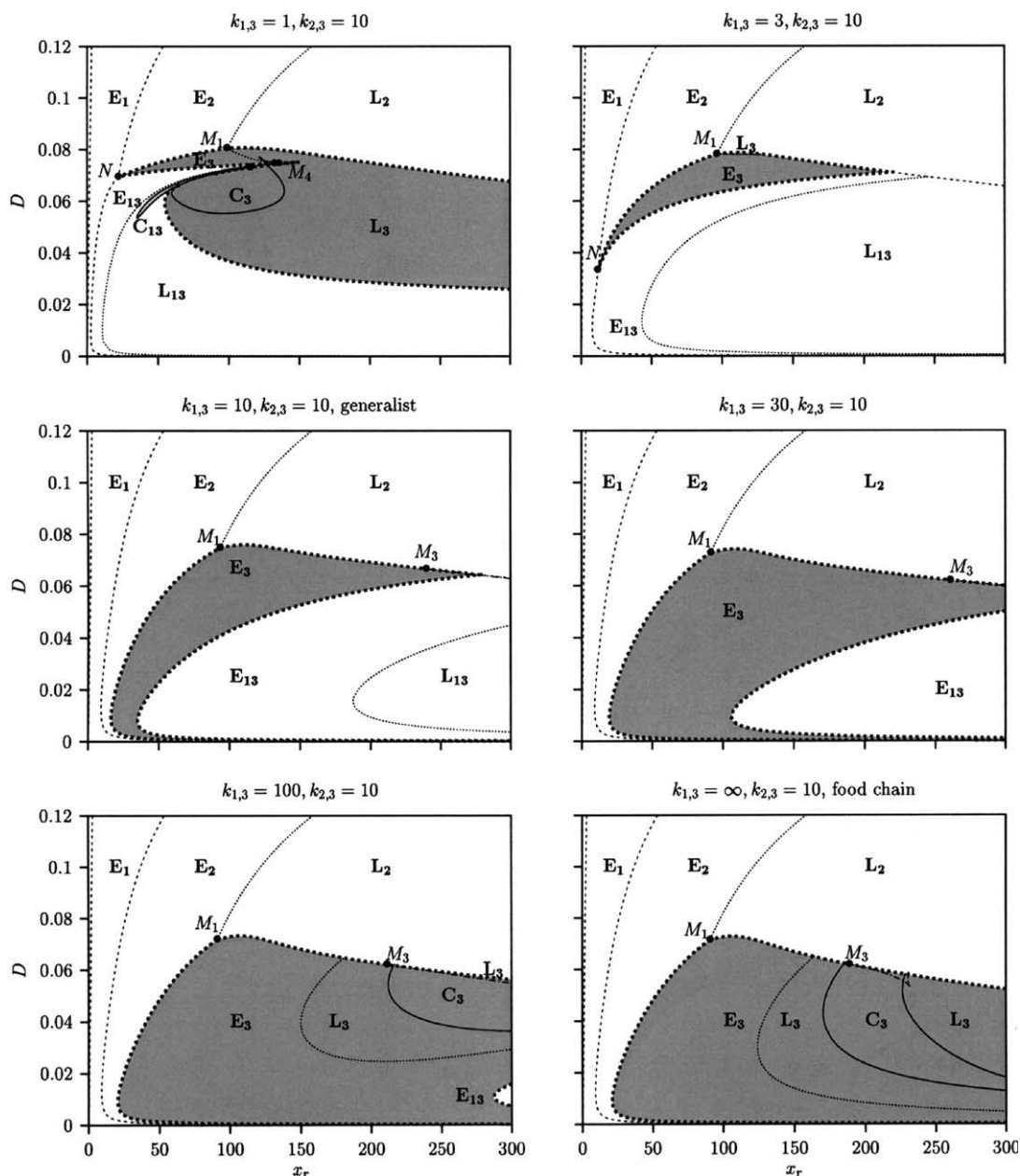


Fig. 12. Bifurcation diagrams where the parameter $k_{1,3}$ for the omnivore–prey trophic interaction is varied: $k_{1,3} = 1, 3, 10, 30, 100, \infty$ where $k_{2,3} = 10$. The gray regions mark coexistence of the three species.

For $k_{1,3} = 1$ there is a codim-2 point N but not for $k_{1,3} = 10$ independent of the value of $k_{2,3}$. Therefore, we try to find a condition for $D^* = 0$, where point N is on the horizontal axis with $x_r = \infty$. With Eq. (8b) the expression for $k_{1,3}$ denoted as $k_{1,3}^*$ becomes

$$\bar{x}_1^* = \frac{m_2 k_{1,2}}{\mu_{1,2} - m_2} \quad \text{and} \quad k_{1,3}^* = \frac{(\mu_{1,3} - m_3) \bar{x}_1^*}{m_3}. \quad (12)$$

Thus

$$k_{1,3}^* = \frac{(\mu_{1,3} - m_3) m_2 k_{1,2}}{(\mu_{1,2} - m_2) m_3}. \quad (13)$$

Hence, for $k_{1,3} > k_{1,3}^*$, $k_{1,3}^* = 7.07143$ for the vital parameter values given in Table 4, we have $D^* < 0$ and competitive exclusion gives that the predator out-competes the omnivore for all dilution rates. The top-right panel diagram in Fig. 11 illustrates this. The top-left panel is the diagram Fig. 3 for the competition case. There is coexistence of the predator and omnivore species as a non-equilibrium attractor. In the region L_3 this non-equilibrium attractor is a period-one limit cycle but in the region C_3 it can be higher periodic or chaotic behaviour. Observe that in these regions the limit cycles L_{13} and L_2 on the boundary of the positive orthant are both unstable.

The middle-left panel where $k_{1,3} = 1$ and $k_{2,3} = 10$, the three points N , M_1 and M_4 , are not at one straight line but they mark now the vertex of a triangle like region. In this small region there is persistence in a stable equilibrium E_3 . The middle-right panel next to it is the diagram for the generalist omnivore already explained in Section 3.2.

In the diagram in the bottom-left panel where $k_{2,3} = 1$ the point M_1 moved further upwards and the point M_4 moved to the right, outside the x_r -range of the diagram. This increases the region with persistence of the three species. In the bottom-right diagram the point M_1 moved to a point with dilution rate above $D = 0.12$. Here the region of persistence is very large for rather large dilution rates, however, now in a substantial part, region L_3 , only as a non-equilibrium attractor.

Comparing the diagrams for $k_{1,3} = 1$ with those for $k_{1,3} = 10$ depicted in Fig. 11 indicates that it is important whether or no the two transcritical bifurcation curves $TC_{e,2}^-$ (invasion of the omnivore, $x_3 = 0$, in the prey–predator bi-trophic food chain, $x_1 \geq 0$, $x_2 \geq 0$), and $TC_{e,13}^-$ (invasion of the predator, $x_2 = 0$, $x_1 \geq 0$, $x_3 \geq 0$, in the prey–omnivore bi-trophic food chain), for the two bi-trophic food chains intersect in codim-2 point N with positive D^* . Observe that in all diagrams the bifurcation curves for the nutrient–prey–predator system are the same. This helps to find the codim-2 points M_1 and N since they lie on these curves. These results show that the position of the point M_1 depends strongly on the $k_{2,3}$ value, especially when $k_{1,3}$ is large. The position of point N does not depend on $k_{2,3}$ since this point is fixed by the mutual independent interactions between the predator and prey, and omnivore and prey, thus parameters $k_{1,2}$ and $k_{1,3}$.

Fig. 12 shows the influence of the parameter $k_{1,3}$ where in all diagrams $k_{2,3} = 10$. In the top-left diagram with $k_{1,3} = 1$ the omnivore consumes the prey most. There are three codim-2 bifurcation points, N , M_1 and M_4 . The region of coexistence E_3 is an attracting equilibrium that is enclosed by the three bifurcation curves which connect these points. As in the competition case, there is non-equilibrium coexistence in the region L_3 .

With $k_{1,3} = 3$ there are only two points N , M_1 while point M_4 lies outside the diagram with large x_r value. Non-equilibrium coexistence occurs in a very small part of the diagram in the neighbourhood of point M_1 . In the regions E_{13} and L_{13} the nutrient–prey–predator food chain has a stable limit cycle, L_2 , but the omnivore is able to invade and when it approaches the equilibrium E_{13} or limit cycle L_{13} the predator is replaced by the omnivore, see Fig. 7 (middle, bottom). The area of the region with equilibrium coexistence is larger than with $k_{1,3} = 1$.

With $k_{1,3} = 10$, the D -value for the bifurcation point N is negative, that is, point N does not exist. In this diagram another codim-2 point appears, M_3 . Close to that point, stable limit cycles for the whole food web occur, but the region where this happens is small, see also Fig. 9.

With $k_{1,3} = 30$ the region E_3 is rather large but the omnivore out-competes the predator in still a rather large part, region E_{13} of the diagram. With $k_{1,3} = 100$ the region where the omnivore and prey coexist is small. However, besides an interior equilibrium in region E_3 , there is also non-equilibrium coexistence in the regions L_3 and C_3 . With $k_{1,3} = \infty$, the food chain case, the omnivore preys only on the predator. The region with non-equilibrium coexistence increased with respect to the $k_{1,3} = 100$ case.

5. Discussion

In [27,28] a nutrient–two-prey–predator food web is analyzed using bifurcation analysis. Generally, in the absence of the predator, one prey can invade and establish itself while the other is eliminated: this is called competitive exclusion. It was shown that the bifurcation point where the two transcritical curves intersect is an important point in the bifurcation diagram for the food web. Here we have a similar situation. The position of the codim-2 bifurcation point N depends only on the parameters that determine the trophic interaction between the predator–prey and omnivore–prey separately, and consequently not on the mutual predator–omnivore interaction. This is a form of bottom-up control of the community.

For this small-scale food web there are 16 parameters which describe the dynamics of the species and their interaction, and 2 control parameters. The two parameters, $k_{1,3}$ and $k_{2,3}$ are directly related to omnivory. Unfortunately the resulting variations due to the change of these two parameters depend also on the other 14 parameters.

We mention the effect of the yield $y_{1,3}$ and maximum growth rate $\mu_{1,3}$ which are changes simultaneously such that in all cases $I_{1,3} = I_{2,3}$. In this paper we assume $y_{1,3} = y_{1,2}y_{2,3} < y_{2,3}$ so that the prey–omnivore conversion efficiency from prey via the predator into omnivore is the same as when prey is directly consumed by the omnivore. For instance, consider the case where the efficiencies of the omnivore consuming the predator and the prey are the same, that is $y_{1,3} = y_{2,3}$ and consequently $\mu_{1,3} = \mu_{2,3}$, while all other parameters are those of the generalist shown in Table 4. Then, the prey–omnivore chain is more efficient than prey–predator–omnivore chain when conversion from prey into omnivore is concerned. We found that even in this case the region with equilibrium coexistence for $k_{1,3} = 100$ is slightly larger than for the food chain case $k_{1,3} = \infty$. When $y_{1,3} > y_{2,3}$ and consequently $\mu_{1,3} > \mu_{2,3}$ the omnivore–prey system dominates especially when D is small and x_r is large, similar to the generalist case (Figs. 11 and 12).

This shows that the sensitivity analysis performed here, does not give a complete picture of the consequences of omnivory on the dynamics of the food web in general. In this paper the ‘basis’ parameter values are based on experimental data for a microbial food web; a carbohydrate-limited substrate, bacterial prey and protozoan predator, while in [2,11] the parameter values determined by the body sizes and for the metabolic categories (endotherm, vertebrate ectotherm and invertebrate) delineated in [29]. Thus, different consequences of omnivory are to be expected.

In [11] the parameter ω is referred to as the strength of omnivory, suggesting that it is a measure for omnivory. However, the calculated diagrams given in [11] depend also on their second

parameter, $k_{1,3}\omega$. The fact that some features of the bifurcation diagram are best described by the two parameters $k_{1,3}$ and $k_{2,3}$, for instance the existence of point N , motivate us to use these two parameters as a measure for omnivory.

The end-point, the established community, depends on the order in which the predator and omnivore are introduced into the nutrient–prey system in stable equilibrium. We study the dynamics of the bounded system (2) in the positive orthant $\mathbb{R}_+^4$. Persistence means that the attractor is in the interior of this orthant. With omnivory multiple attractors coexist with possibly attractors on the two boundaries of the positive orthant $\mathbb{R}_+^4$. These are the invariant subspaces where $x_2 = 0$ and $x_3 = 0$. Invasion is possible when the invariant set in such an invariant subspace is only attracting in the positive orthant $\mathbb{R}_+^3$ associated with the non-invaded system, that is where the invader is not taken into account, but non-attracting in the orthant $\mathbb{R}_+^4$ associated with the invaded system, that is where the invader is taken into account even when its biomass is zero on the boundary $\text{bd } \mathbb{R}_+^4$. Different non-trivial situations can occur with invasion of the predator or omnivore:

- Two boundary invariant sets in the subspaces $x_2 = 0$, E_{13} or L_{13} , and $x_3 = 0$, L_2 , respectively. One invariant set is unstable and the other stable. This gives replacement of the resident species by the invader, $L_2 \rightarrow E_{13}$, Fig. 7 (middle) or $L_2 \rightarrow L_{13}$, Fig. 7 (bottom).
- Three invariant sets. Two are on the boundary of the orthant in the subspaces $x_2 = 0$, E_{13} , and $x_3 = 0$, L_2 , respectively and both are unstable. The third is the stable interior invariant set, E_3 , L_3 or C_3 . When invasion occurs via both boundary invariant sets the system converges to the interior attractor, $E_{13} \rightarrow E_3$, Fig. 10 (top) and $L_2 \rightarrow E_3$, Fig. 7 (top).
- Four invariant sets. Two are on the boundary of the orthant in the subspaces $x_2 = 0$ and $x_3 = 0$, respectively, at least one is stable in this case L_2 is stable and E_{13} is unstable. Two are in the interior, one unstable L_3 and one stable E_3 , L_3 or C_3 . The stable manifold of the unstable limit cycle L_3 is the separatrix between L_2 and E_3 , see Fig. 9. When invasion occurs the system converges to the interior attractor $E_{13} \rightarrow E_3$, Fig. 10 (top) or to the other boundary attractor $E_{13} \rightarrow L_2$, Fig. 10 (bottom).

With the assumption that the predator is introduced first, the sequence as well as the end-point are unique.

Other type of heteroclinic connections in low dimensional ecological systems are investigated in the literature. Heteroclinic cycles in related three species food web models were investigated in [22,23]. For the three species food chain case ($k_{1,3} = \infty$), a heteroclinic connection between the interior saddle equilibrium and the saddle limit cycle is in [30] related to a complicated shape of the domain of attraction of an interior stable limit cycle or chaotic attractor.

6. Conclusions

The influence of omnivory was investigated using bifurcation analysis of our model at variable feeding behaviours of the omnivore. Two limiting cases where the omnivore acts as a specialist, competition and a food chain, figured as starting points. Competition was analyzed by considering the two resource–prey–competitor systems separately. In the analysis of these bi-trophic

food chains we encountered chaos for plausible parameter values. This innovative result will be dealt with in a forthcoming paper.

In terms of non-linear dynamic system theory, an assembly sequence is formed by a series of connections between equilibria or limit cycles. These are connections between saddle equilibria or limit cycles at the boundary of the positive orthant, except when there is convergence to a positive and stable equilibria or limit cycle where all species persist at the invulnerable resistant end-point.

For the competition case we derived criteria for coexistence of the omnivore and predator. When this condition is met, survival of the two populations on the common prey is possible, only as a non-equilibrium attractor. This occurs at rather high dilution rates and moderate nutrient concentrations in the supply. The generalist omnivore can coexist in equilibrium with the other species in a relatively large part of the diagram. Further reduction of the predation pressure by the omnivore on the prey gives first a larger region but then it declines somewhat until no prey is consumed by the omnivore as in the food chain. Hence, a weak trophic strength between the omnivore and the prey is advantageous. This is partly in agreement with work by McCann et al. [2] where they suggest that weak interactions are essential for community persistence.

The key results are:

- With a mass balance formulation where nutrients are modelled explicitly, a predator–prey system in the chemostat can show chaotic behaviour for plausible parameter values.
- When the omnivore and the predator are competitors for the common prey, coexistence occurs only as a non-equilibrium attractor.
- A heteroclinic connection from a saddle equilibrium to a saddle limit cycle separates regions in the bifurcation diagram with different attractors to which the system evolves after invasion.
- The results for a microbial food web in the chemostat indicate that a weak trophic strength between the omnivore and the prey is advantageous.
- Generally, for the vital parameter chosen here, the omnivore–prey system dominates for low dilution rates and high nutrient inflow rates, the predator–prey system for high dilution rates and low nutrient inflow rates, while the three species coexist for moderate values.

We consider only invasion of the omnivore in the existing prey–predator system and study omnivory by variation of the saturation constants of the multi-species functional response, as used in the description of the trophic interactions between the omnivore and its prey. We recall that all results with respect to the role of omnivory depend also on the vital parameters, as given in Table 4, which were kept constant. Hence, general statements about the role of omnivory are problematic. We mention the following example. With $y_{1,3} \leq y_{2,3}$ we found that the region with equilibrium coexistence for $k_{1,3} = 100$ is slightly larger than for the food chain case $k_{1,3} = \infty$. However, when $y_{1,3} > y_{2,3}$ and consequently $\mu_{1,3} > \mu_{2,3}$, since we assume $I_{1,3} = I_{2,3}$, that is the omnivore assimilates the prey more efficient than the predator, equilibrium coexistence with $k_{1,3} = 100$ occurs in a smaller region of the two-parameter diagram than for the food chain case $k_{1,3} = \infty$ instead of slightly larger. As a result a weak trophic strength between the omnivore and the prey is not advantageous when $y_{1,3} > y_{2,3}$.

Application of numerical bifurcation analysis is feasible in a similar context for interactions in food chains studied in [2,31,32]. This is a next step towards the analysis of natural, and more complicated, food webs. The variety of the dynamic behaviours we encountered indicates that

the complete analysis of large-scale or even intermediate-scale food webs on a routine basis is practically not feasible. When the focus is on applications, for instance conservation and management problems of natural communities where the range of parameter values involved is small, the approach proposed in this paper might prove beneficial.

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Appendix A. Calculation of the heteroclinic connection

In the generalist case we found a global bifurcation denoted by $G_{e,c}^\#$ depicted in Fig. 6. In this appendix the algorithm is given to calculate the heteroclinic connecting orbits. We use a boundary-value method described in [15,25,33–36]. The heteroclinic problem is truncated into a finite time interval and certain boundary conditions at the end points of that interval are imposed. Suitable boundary conditions are obtained by using linear approximations near the equilibrium point E_{13} and the limit cycle L_2 .

The continuation of the codim-1 bifurcation curve $G_{e,c}^\#$ in the two-parameter diagram is computed by solving simultaneously 21 scalar equations for 22 scalar variables.

Nine equations are associated with the linear approximations near the equilibrium point E_{13} . Eqs. (2a)–(2d) with zero right-hand side fix the equilibrium point $\mathbf{x}$. If the system is described by $d\mathbf{z}/dt = \mathbf{f}(\mathbf{z})$ where $\mathbf{f} : \mathbb{R}_+^4 \rightarrow \mathbb{R}_+^4$ (the system is autonomous, hence there is no explicit dependency on time t), then the equilibrium is determined by the four equations

$$\mathbf{f}(\mathbf{x}) = 0. \quad (\text{A.1})$$

Five equations fix the normalized eigenvector $\mathbf{p} \in \mathbb{R}^4$ and the positive eigenvalue λ of the Jacobian matrix $\mathbf{J}$ evaluated at $\mathbf{x}$. This eigenvalue λ is just the invasion criterion for invasion of the predator. The equations read

$$\mathbf{J}\mathbf{p} = \lambda\mathbf{p}, \quad (\text{A.2})$$

$$\langle \mathbf{p}, \mathbf{p} \rangle = 1, \quad (\text{A.3})$$

where $\langle \mathbf{r}, \mathbf{s} \rangle = \mathbf{r}^T \mathbf{s}$ is the standard scalar product in $\mathbb{R}^4$.

Further nine equations are associated with the linear approximations near the limit cycle L_3 . Let the flow $\phi(t, \mathbf{x})$, $\phi : \mathbb{R} \times \mathbb{R}_+^4 \rightarrow \mathbb{R}_+^4$, denote a solution of system (2a)–(2d) so that $\phi(0, \mathbf{x}) = \mathbf{x}$. The cross-section Σ is defined by

$$\Sigma = \left\{ \mathbf{x} \in \mathbb{R}_+^4 : \frac{\mu_{1,3} - D_3}{k_{1,3}} x_1 + \frac{\mu_{2,3} - D_3}{k_{2,3}} x_2 = D_3 \right\}.$$

Then the *Poincaré map* $P : \Sigma \rightarrow \Sigma$ is defined for a point $\mathbf{z} \in \Sigma$ by $P(\mathbf{z}) = \phi(\tau, \mathbf{z})$, where $\tau = \tau(\mathbf{z})$ is the time taken for the orbit $\phi(t, \mathbf{z})$ to first return to Σ .

The next five equations determine the fixed point $\mathbf{y}$ of the Poincaré map of the limit cycle L_3 defined in Σ

$$\mathbf{y} = P(\mathbf{y}), \quad (\text{A.4})$$

$$\mathbf{y} \in \Sigma. \quad (\text{A.5})$$

Eq. (A.5) is the phase condition. On the saddle limit cycle we have $T_0 = \tau(\mathbf{y})$. The monodromy matrix associated with the saddle limit cycle L_3 [25] is denoted by $\mathbf{M}$. The following four equations fix the normalized adjoint eigenvector $\mathbf{q} \in \mathbb{R}^4$ and one equation the eigenvalue of $\mathbf{M}$ denoted by ρ , being the single multiplier of the Poincaré map with magnitude greater than 1.

$$\mathbf{M}^T \mathbf{q} = \rho \mathbf{q}, \quad (\text{A.6})$$

$$\langle \mathbf{q}, \mathbf{q} \rangle = 1. \quad (\text{A.7})$$

The remaining two equations are associated with the boundary-value problem. The truncated heteroclinic orbit starts at a fixed distance from the point $E_{13} = \mathbf{x}$ on the linear approximation $T^u(\mathbf{x})$, of the unstable manifold $W^u(\mathbf{x})$ fixed by the eigenvector corresponding to the positive eigenvalue of the Jacobian evaluated at $\mathbf{x}$. Then the set of coupled ODES (2) which describe the dynamic system, is solve numerically using a Runge–Kutta method for a fixed time period T_h which acts as a free parameter during the continuation process. The two equations

$$\langle \phi(T_h, \mathbf{x} + \varepsilon \mathbf{p}) - \mathbf{y}, \mathbf{q} \rangle = 0, \quad (\text{A.8})$$

$$\phi(T_h, \mathbf{x} + \varepsilon \mathbf{p}) \in \Sigma, \quad (\text{A.9})$$

fix the truncated heteroclinic orbit, where $\varepsilon \ll 1$ is a small scalar. Eq. (A.8) ensures that the vector from the fixed point on the limit cycle $\mathbf{y} \in \Sigma$ to the endpoint $\phi(T_h, \mathbf{x} + \varepsilon \mathbf{p}) \in \Sigma$, is perpendicular to the adjoint eigenvector $\mathbf{q}$ of the monodromy matrix $\mathbf{M}$ corresponding to the multiplier, ρ , with magnitude greater than one. The Fredholm alternative [25] gives that the end point is on the linear approximation $T^s(\mathbf{y})$ of the stable manifold $W^s(\mathbf{y})$ of the saddle limit cycle L_3 at point $\mathbf{y}$.

The 22 variables: D , x_r , $\mathbf{x}$, $\mathbf{p}$, λ , $\mathbf{y}$, $\mathbf{q}$, ρ , T_0 , T_h and the 21 equations: (A.1)–(A.9) determine the curve $G_{e,c}^\neq$ in Fig. 6. The continuation of this global bifurcation $G_{e,c}^\neq$ was done by means of a predictor-corrector continuation method with step-size control [25,37,38]. The initial data for the continuation procedure were obtained as follows. With $x_r = 300$ the dilution rate D was changed smoothly and system (2) was solved numerically starting close to the saddle point $E_{13} = \mathbf{x}$ on the linear approximation of the unstable manifold. The point where the asymptotic behaviour changed suddenly (convergence to E_3 instead of L_{13} see Fig. 10) was chosen to start the continuation process.

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