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Omnivory and food web dynamics

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Abstract

Intraguild predation is a trophic interaction in which two consumers compete for one resource and where one of the consumer species may also feed on its competitor. The intraguild predator's diet follows from the relative strength of its interactions with its potential prey. Current view holds that weak interactions between species promote the stability of food webs. To the contrary, nutrient enrichment is predicted to destabilize ecosystems. We present a theoretical analysis of the interplay between intraguild predation and nutrient enrichment in a Marr-Pirt chemostat model of a microbial food web. We perform a two-dimensional bifurcation analysis along a gradient of allochtonous nutrient levels and a gradient of one out of two biologically plausible strategies to explore the spectrum of the intraguild predator's foraging interactions. Both strategies show that intraguild predation may

- stabilize food chains;
- eliminate chaos, predicted by food chain models;
- give rise to multiple stable states;
- be favored in systems with low turn-over rates, where the intraguild predator has a low interaction strength and a low yield on the basal resource.

Keywords: Ecosystem modelling; Intraguild predation; Bifurcation analysis; Multiple stable states; Invasion; Nutrient enrichment

1. Introduction

Nutrient enrichment has been shown, both empirically and theoretically, to affect ecosystems in several ways (DeAngelis, 1992; Scheffer et al., 1993; Abrams and Roth, 1994). For instance, known as the 'paradox of enrichment', it may reduce species diversity and ecosystem functioning (Rozenzweig, 1971). As early as the sixties, food chain models were analysed at variable production levels (Rozenzweig and MacArthur, 1963). Since then, a variety of modelling studies have predicted that nutrient enrichment can lead to complex dynamics, as well as extinctions of species (Abrams, 1993; Leibold et al., 1997; Ghosh and Sarkar, 1998; Huxel and McCann, 1998; Vayenas and Pavlou, 1999a; Persson et al., 2001).

The theoretical study on the effects of nutrient enrichment has long been limited to linear food chains. The explanation lies in the history of food web modelling studies. In the late 1970s, Pimm and Lawton simulated a large number of food webs including omnivorous links, as non-linear interactions (Pimm and

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Lawton, 1978). They discovered that these additional interactions in general caused stable internal equilibria to become statistically rare. As stable equilibria were deemed essential for the long-term survival of ecosystems, it was concluded that omnivory should be rare in natural food webs.

In the late 1980s, this view became subject of debate, as renewed investigations demonstrated that, in natural systems, omnivory is the rule, rather than the exception (Sprules and Bowerman, 1988; Polis, 1991; Polis and Strong, 1996). As a consequence, a number of theoretical analyses of this interaction have appeared in the last few years. These studies are in general about the simplest conceivable example of omnivory, where a predator species and a consumer species compete for a single resource, while the predator species can also feed on the consumers (McCann and Hastings, 1997; McCann et al., 1998; Diehl and Feißel, 2000, 2001; Mylius et al., 2001; Revilla, 2002). This combination of competition and predation interactions is known as intraguild predation.

One of the general results that derive from recent studies is that whenever certain conditions are met, intraguild predation can promote persistence of food webs. Firstly, the intraguild prey has to be the superior competitor for the common prey, otherwise it will be excluded from the system due to effects of competitive exclusion (Polis et al., 1989). Secondly, the resource availability should be intermediate for coexistence of intraguild predator and intraguild prey, as hypothesized by Holt and Polis (1997) and corroborated by Morin (1999), Diehl and Feißel (2000, 2001), Heithaus (2001), Mylius et al. (2001). If the common resource is scarce, the intraguild prey may outcompete its predator. On the other hand, if it becomes too abundant, the intraguild prey may not survive the predation pressure of the omnivore. Thirdly, Bondavalli and Ulanowicz (1999) showed that, due to positive effects on the basal prey, strong omnivorous predation on the intraguild prey in combination with weak predation on the common prey may foster the persistence of intraguild configurations. In Pimm and Lawton's model experiments, these conditions were not always met.

In this paper, we will present a model which lends itself to explore the complete spectrum of intraguild predation, from competitive to predacious interactions, at variable nutrient enrichment levels. As omnivorous interactions are to a large extent determined by the catching efficiencies and yields, we will focus on the particular influence of these properties on the model dynamics.

The paper is organized as follows. In the next section, we present the model structure and motivate our modelling approach. In the result section, we present a bifurcation analysis of the model to distinguish regions in parameter space that differ in terms of coexistence and stability. In Section 4, we put our results in context and point out implications of the study.

2. Description of the model

Our model describes a simple ecosystem in a chemostat environment. Although we ultimately want to gain insight in natural ecosystems, the study of less realistic, but controllable, ecosystems is a necessary first step. A chemostat system fulfills this requirement: it is spatially well-defined, input and output are known and under experimental control, and through mixing an approximately homogeneous environment can be created. The latter is a prerequisite for the type of modelling involved, in particular the use of the law of mass action to model encounters between predator and prey.

In addition to an abiotic nutrient N, the model describes three species of biota representing different trophic niches: a resource R, intraguild prey C and intraguild predator P. Fig. 1 shows the trophic levels and interactions among these species. The resource feeds on the abiotic nutrient, and is preyed upon by both intraguild prey and predator. The latter not only predates on the resource, but also on the intraguild prey; it is not subject to predation itself. As the intraguild predator feeds on two different trophic levels, it cannot be attributed to a particular trophic level per se. For this reason, we use trophic niche rather than trophic level to indicate the position of the omnivore in the food web (cf. Levine, 1980).

The following Marr-Pirt (Marr et al., 1962) system describes the interactions among the participants:

$$\frac{\mathrm{d}}{\mathrm{d}t}N = (\boldsymbol{N_r} - N)\boldsymbol{D} - \frac{a_{N,R}N}{1 + a_{N,R}b_{N,R}N}R \tag{1a}$$

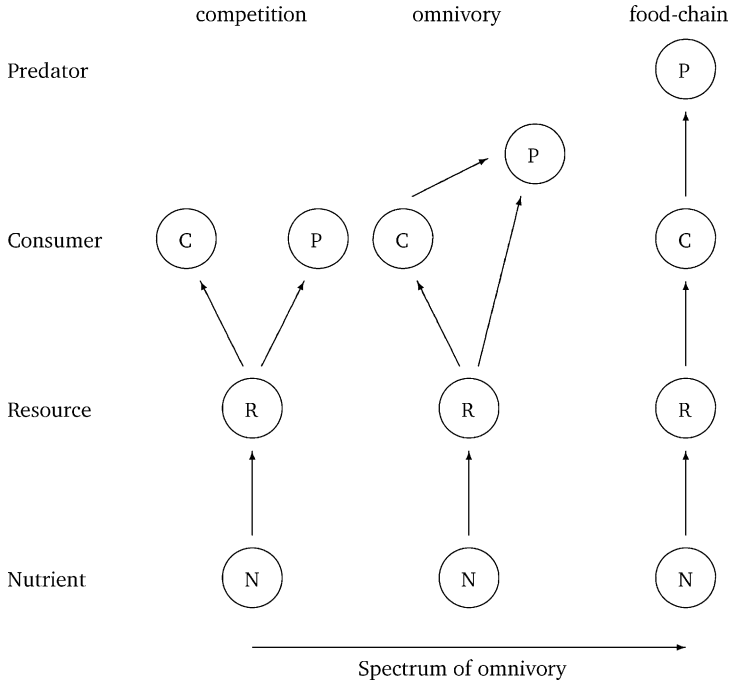

Fig. 1. Representation of the studied trophic interactions. The circles denote the different trophic niches. Abiotic resources are denoted by N, while R, C and P represent resources, consumers and predators, respectively. The architecture of the food web depends on the feeding behavior of the highest trophic level. This architecture may vary from a competition food web, where P consumes R exclusively, via a spectrum of omnivory interactions, to the linear food chain, where P only feeds on C.

$$\frac{\mathrm{d}}{\mathrm{d}t}R = R\left(\frac{y_{N,R}a_{N,R}N}{1+a_{N,R}b_{N,R}N} - \boldsymbol{D} - m_R\right) - \frac{a_{R,C}R}{1+a_{R,C}b_{R,C}R}C - \frac{a_{R,P}R}{1+a_{R,P}b_{R,P}R+a_{C,P}b_{C,P}C}P \tag{1b}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}C = C\left(\frac{y_{R,C}a_{R,C}R}{1+a_{R,C}b_{R,C}R} - \boldsymbol{D} - m_C\right) - \frac{a_{C,P}C}{1+a_{R,P}b_{R,P}R+a_{C,P}b_{C,P}C}P \tag{1c}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}P = P\left(\frac{y_{R,P}a_{R,P}R + y_{C,P}a_{C,P}C}{1+a_{R,P}b_{R,P}R+a_{C,P}b_{C,P}C} - \boldsymbol{D} - m_P\right) \tag{1d}$$

Table 1 summarizes the notation in the mathematical model. The parameter $\boldsymbol{N_r}$ is the reservoir density, i.e. the concentration of the non-living nutrient in the medium supplied to the chemostat. The throughput rate $\boldsymbol{D}$ is the supply rate relative to the volume of the chemostat. These parameters are under control of an experimenter. They are set in bold type to distinguish them from parameters that relate to the physiology of the biota in the chemostat and can not be controlled. The parameters m_Y represent the costs for maintenance per unit of time of species Y. Parameters with two subindices separated by a comma (X, Y) involve an interaction between two species, the consumer Y and its food X. Here, $a_{X,Y}$ is the catching rate of species Y feeding on X, $y_{X,Y}$ is the corresponding yield and $b_{X,Y}$ is the handling time, characteristic for the type-II functional response (Holling, 1965).

When the intraguild predator is handling one type of prey, it temporarily cannot catch the other. Therefore, the functional responses that deal with the intraguild predator's consumption involve the densities of both the resource and the intraguild prey species. This two–prey functional response was first introduced

Table 1
Parameters and state variables

Parameter	Dimension	Units	Interpretation
$\boldsymbol{D}$	t^{-1}	h^{-1}	Throughput rate
$\boldsymbol{N_r}$	$m\,v^{-1}$	$mg\,dm^{-3}$	Substrate concentration in reservoir
$a_{X,Y}$	$v\,m^{-1}\,t^{-1}$	$dm^3\,mg^{-1}\,h^{-1}$	Catching rate
$b_{X,Y}$	t	h	Handling time
$y_{X,Y}$	$m\ m^{-1}$	$mg\,mg^{-1}$	Mass coupling coefficient
m_Y	t^{-1}	h^{-1}	Maintenance rate coefficient
t	t	h	Time
N	$m\,v^{-1}$	$mg\,dm^{-3}$	Substrate density
R, C, P	$m\,v^{-1}$	$mg\,dm^{-3}$	Biomass density

t: time, m: biomass, v: volume of the reactor. The index Y denotes the trophic level. Some parameters, for instance the saturation constants $k_{X,Y}$, have double indices separated by a comma to emphasize that these quantities depend on two levels. Here, Y is the species that feeds upon X.

by Murdoch (1973) and expanded on by Cock (1978) and Chesson (1983). In the model, the omnivore does not effectively select for either prey by preference. This applies well to the foraging behavior of zooplankton (Legović, 1989).

We want to know how the long-term behavior of the model depends on the intraguild predation interactions as well as on the nutrient provision. To this end we will perform bifurcation analysis of system (1). For an introduction to bifurcation analysis the reader is referred to Guckenheimer and Holmes (1985), Kuznetsov (1998), and to Bazykin (1998) for the application to ecosystem models. 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. When such a parameter is varied, a value at which the asymptotic dynamics changes abruptly (for instance the solution becomes a stable limit cycle instead of a stable equilibrium) is called a bifurcation point. In this study, we use two-dimensional bifurcation analysis, in which two parameters are varied simultaneously. Here, bifurcation curves separate regions in the two-dimensional parameter space, which differ in qualitative asymptotic behavior. We perform the bifurcation analyses with the computer programs AUTO (Doedel et al., 1997) and LOCBIF (Khibnik et al., 1993).

We concentrate on two aspects of the long-term behavior, coexistence and invasibility. In correspondence to Grimm and Wissel's (1997) nomenclature, we define coexistence as the potential of the intraguild predator and intraguild prey to jointly persist. Invasibility implies that a species, upon entering the system in arbitrarily small numbers, will increase in number and stays in the system. These concepts correlate but are not identical. If both intraguild predator and intraguild prey can persist at a given set of parameter values, this does not guarantee that either one can invade when it is not already present. Conversely, successful invasion of a species may not always result in coexistence. One species may also simply replace the other. To understand long-term dynamics and community assembly, both aspects must be taken into account.

The effect of an omnivory interaction depends on the foraging behavior of the intraguild predator. In the model, this behavior is controlled by the catch rates $a_{R,P}, a_{C,P}$ and the handling times $b_{R,P}, b_{C,P}$. The catch rates characterize the predation ability of the intraguild predator on the resource and intraguild prey, respectively, whereas the handling times determine the maximum ingestion rates with respect to each particular prey. In our analyses, we will use the catching rates to explore the effect of omnivory in the food chain.

As part of their study, Mylius et al. (2001) performed a bifurcation analysis with the two catch rates as simultaneously varied parameters. In this way, they were able to cover the complete spectrum of omnivorous interactions. They demonstrated that only in a small region of parameter space, where $a_{R,P}$ is relatively low, coexistence of the intraguild predator and intraguild prey can prevail. Their model differs from ours in that it concerns a semi-chemostat environment in which a resource species, and not a non-living

nutrient, forms the base of the food chain. This implies that our model is four-dimensional (N, R, C, P) whereas theirs is three-dimensional (R, C, P). We will test whether their conclusions hold for our model as well.

Our aim is to weigh the effect of omnivorous interactions against the effect of nutrient enrichment. The latter is modelled through variation of the nutrient inlet density $\boldsymbol{N}_\mathbf{r}$ in Eq. (1a), which describes the dynamics of the non-living nutrient density. Consequently we have three parameters of interest, the catch rates $a_{R,P}$, $a_{C,P}$ and the nutrient inlet concentration $\boldsymbol{N}_\mathbf{r}$.

A qualitative analysis of the behavior of system (1) using three bifurcation parameters is mathematically possible, but a graphical representation of results is cumbersome. There are a number of options to circumvent this problem, some of which brought into practice by other authors (McCann and Hastings, 1997; Kooi et al., 2002).

In their studies, McCann and Hastings (1997) and McCann et al. (1998) combine the two catch rates into a single parameter, ω, defined as

$$\omega = \frac{a_{R,P}}{a_{R,P} + a_{C,P}} \tag{2}$$

to specify the interaction strength of the omnivore and its prey types. When $\omega = 0$, $a_{R,P} = 0$, the highest trophic level does not feed on the resource species and effectively figures as a top predator species in a linear food chain. When $\omega = 1$, $a_{C,P} = 0$, so that the highest level ceases to feed on the consumer species. Instead, it now figures as a second consumer, competing with the other consumer for the resource species. At intermediate values of ω, the highest trophic level feeds on both species and, therefore, is an intraguild predator. Thus, $1-\omega$ indicates the trophic distance between the intraguild predator and the consumer species (Levine, 1980). In their analyses McCann and Hastings kept the sum of the two catch rates constant. The corresponding biological interpretation is that intraguild predators have a limited time-budget in which predation efforts on the one prey balance against predation efforts on the other. In our study, we will extend their work by testing this approach at variable allochtonous nutrient input levels.

Recently, Kooi et al. (2002) performed a bifurcation analysis of model (1) in which they used sets of mutually independent catch rates at variable nutrient inputs. They left out assumptions on time budgets and thus had the freedom to vary both catch rates independently. Hence, they were able to assess effects of a larger class of omnivorous interactions. However, as this setup requires two independent and unbounded parameters to determine the degree of omnivory, this approach does not lend itself to explore a spectrum of omnivorous interactions.

In pursuit of the effect of nutrient enrichment in food webs with intraguild predation, we will analyse system (1) at a range of $\boldsymbol{N}_\mathbf{r}$ values, using two different biologically plausible strategies, which can be used to establish a spectrum of intraguild predation interactions. To start with, analogous to McCann and Hastings (1997), we will use the time budget strategy. Here we use ω from 0 (linear food chain) to 1 (competition). To this end, system (1) can be rewritten into

$$\frac{\mathrm{d}}{\mathrm{d}t}N = (\boldsymbol{N}_\mathbf{r} - N)\,\boldsymbol{D} - \frac{a_{N,R}N}{1 + a_{N,R}b_{N,R}N}R \tag{3a}$$

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}R = {} & R\left(\frac{y_{N,R}a_{N,R}N}{1 + a_{N,R}b_{N,R}N} - \boldsymbol{D} - m_R\right) \\ & - \frac{a_{R,C}R}{1 + a_{R,C}b_{R,C}R}C \\ & - \frac{\omega R}{k_\omega + b_{R,P}\omega R + b_{C,P}(1-\omega)C}P\end{aligned} \tag{3b}$$

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}C = {} & C\left(\frac{y_{R,C}a_{R,C}R}{1 + a_{R,C}b_{R,C}R} - \boldsymbol{D} - m_C\right) \\ & - \frac{(1-\omega)C}{k_\omega + b_{R,P}\omega R + b_{C,P}(1-\omega)C}P\end{aligned} \tag{3c}$$

$$\begin{aligned}\frac{\mathrm{d}}{\mathrm{d}t}P = {} & \\ & P\left(\frac{y_{R,P}\omega R + y_{C,P}(1-\omega)C}{k_\omega + b_{R,P}\omega R + b_{C,P}(1-\omega)C} - \boldsymbol{D} - m_P\right),\end{aligned} \tag{3d}$$

where $k_\omega = \left(a_{R,P} + a_{C,P}\right)^{-1}$.

Next, we will analyze an alternative strategy in which the time budget assumption is extended with an efficiency trade-off. Here, a shift in the intraguild predator's foraging behavior in terms of catch rates is corrected for by the difference in yields on both prey types. The ecological interpretation behind this is that

an omnivore feeding mainly on a less profitable resource will have to search more intensively for food than one that feeds on more profitable foods. By this extention of the time budget assumption we add a realistic property to model (3). In the model, we will use compound parameter ζ, which is defined as

$$\zeta = \frac{a_{R,P} y_{R,P}}{a_{R,P} y_{R,P} + a_{C,P} y_{C,P}}, \tag{4}$$

and resembles ω in the sense that when $\zeta = 0$, we have a food chain and when $\zeta = 1$, we have exploitative competition. Here, $1-\zeta$ is the trophic distance between the intraguild predator and the consumer species. Substitution of Eq. (4) into system (1) yields

$$\frac{\mathrm{d}}{\mathrm{d}t}N = (\boldsymbol{N}_\mathbf{r} - N)\boldsymbol{D} - \frac{a_{N,R}N}{1 + a_{N,R}b_{N,R}N}R \tag{5a}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}R = R\left(\frac{y_{N,R}a_{N,R}N}{1 + a_{N,R}b_{N,R}N} - \boldsymbol{D} - m_R\right) - \frac{a_{R,C}R}{1 + a_{R,C}b_{R,C}R}C - \frac{(1/y_{R,P})\zeta R}{k_\zeta + (b_{R,P}/y_{R,P})\zeta R + b_{C,P}/y_{C,P}(1-\zeta)C}P \tag{5b}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}C = C\left(\frac{y_{R,C}a_{R,C}R}{1 + a_{R,C}b_{R,C}R} - \boldsymbol{D} - m_C\right) - \frac{1/y_{C,P}(1-\zeta)C}{k_\zeta + b_{R,P}/y_{R,P}\zeta R + b_{C,P}/y_{C,P}(1-\zeta)C}P \tag{5c}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}P = P\left(\frac{\zeta R + (1-\zeta)C}{k_\zeta + (b_{R,P}/y_{R,P})\zeta R + b_{C,P}/y_{C,P}(1-\zeta)C} - \boldsymbol{D} - m_P\right), \tag{5d}$$

where $k_\zeta = (a_{R,P}y_{R,P} + a_{C,P}y_{C,P})^{-1}$. The compound parameters ω and ζ will be referred to as interaction parameters in the rest of the paper.

In the study of trade-off mechanisms, a proper insight in the role of yields is a prerequisite. We initially conjecture the corresponding parameter values from linear food chain data, so we expect the margin of error to be large. Still, it is of ecological importance and it may well influence our model's dynamic behavior. Therefore, we will analyze the influence of the yields of the shared resource to intraguild predator biomass for both strategies.

Table 2 lists the values of the model parameters used in our simulations. Except for the parameters of the intraguild predator, the values are those of a microbial food chain with ciliates and bacteria, presented by Nisbet et al. (1983) and Cunningham and Nisbet (1983). As an initial step, we infer the values of the intraguild predator's parameters from those of the top-predator, on the assumption that growth rate decreases with trophic distance. We quantify this idea by taking the direct biomass conversion from resource to intraguild predator ($R \to P$) equally efficient as the indirect conversion from resource via intraguild prey to intraguild predator ($R \to C \to P$). This approach is also followed by Diehl and Feißel (2000).

Table 2
Parameter set for bacterium-ciliate models, derived from Cunningham and Nisbet (1983) and Nisbet et al. (1983)

Parameter (unit)	Values			
	$Y = R$, $X = N$	$Y = C$, $X = R$	$Y = P$	
			$X = R$	$X = C$
$a_{X,Y}$ ($\mathrm{dm^3\,mg^{-1}\,h^{-1}}$)	0.156	0.037	Varies	Varies
$b_{X,Y}$ (h)	0.8	3.0	4.0	4.0
$y_{X,Y}$ ($\mathrm{mg\,mg^{-1}}$)	0.4	0.6	Varies	0.6
m_Y ($\mathrm{h^{-1}}$)	0.025	0.01	0.0075	

The values for the parameters m_X are given as well. The range of nutrient supplies is $0 < \boldsymbol{N}_\mathbf{r} \leq 300\,\mathrm{mg\,dm^{-3}}$.

3. Model dynamics

This section contains the bifurcation diagrams that describe the long-term qualitative behavior of systems (3) and (5) as a function of nutrient provision and the intraguild predator's feeding properties. We present an integrated analysis of both the time-budget and the trade-off model, and we also investigate the influence of the yield.

To start with, we will describe the different kinds of qualitative behavior we may encounter. In the paragraphs thereafter, the bifurcation diagrams will be described and compared. We will concentrate on differences in invasibility and persistence of the intraguild predator and prey, and to a lesser extent on non-equilibrium dynamics, which are well-known to emerge from food chain models.

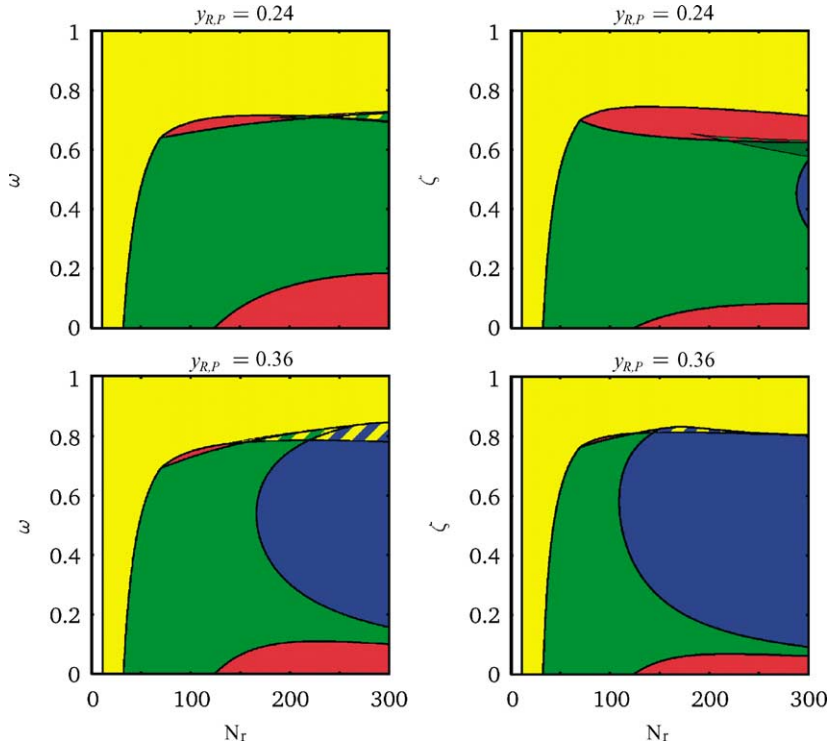

Fig. 2. Bifurcation diagrams of the timebudget model (left positions) and the trade-off model (right positions) at $y_{R,P} = 0.24, 0.36$. Different colors refer to differences in asymptotic qualitative behavior. Yellow: N–R–C, blue: N–R–P, bright green: N–R–C–P in equilibrium, dark-green: two attractors for N–R–C–P in equilibrium, red: N–R–C–P in non-equilibrium, dashed: two attractors of corresponding colors. Parameter values are as indicated in Table 2, $\boldsymbol{D} = 0.03$. Pure competition implies $\omega, \zeta = 1$, whereas $\omega, \zeta = 0$ corresponds to a linear food chain.

3.1. Model behavior typology

The results of our analyses are presented in Figs. 2–4. In these figures, the concentration of the abiotic nutrient in the inflow $\boldsymbol{N_r}$ is on the horizontal axis. The omnivore's feeding strategy parameter is on the vertical axis. This parameter can be either ω or ζ, depending on which strategy is used. For comparison, both ω and $\zeta = 0$ correspond with a linear food chain, whereas when ω and $\zeta = 1$, C and P interact solely through competition for the common resource. All values in between delineate intraguild predation.

The bifurcation diagrams consist of curves that separate the parameter space into a number of regions. For each point within such an area, the qualitative asymptotic behavior of the model is identical, although the quantitative solutions may differ considerably. When we discuss the dynamics of different area's we will concentrate on the qualitative behavior, and on two aspects in particular. Firstly, we will analyse the system's persistence and analyse which trophic niches can be invaded. Secondly, we will, to some degree, analyse the attractor type. This is only done for model solutions in which all trophic niches are occupied. Moreover, we do not analyse these non-equilibrium attractors in any further detail, as this would complicate the analysis considerably, without bearing relevance to our study. We will use the term 'complex dynamics' in reference to those regions.

In the bifurcation diagrams, all regions with identical qualitative behavior are colored in the same fashion. Unpatterned regions correspond to parameter values at which the system has a single attractor; shaded regions refer to parameter values at which there are two attractors. The different colors mark the particular attractor types, in terms of resident species,

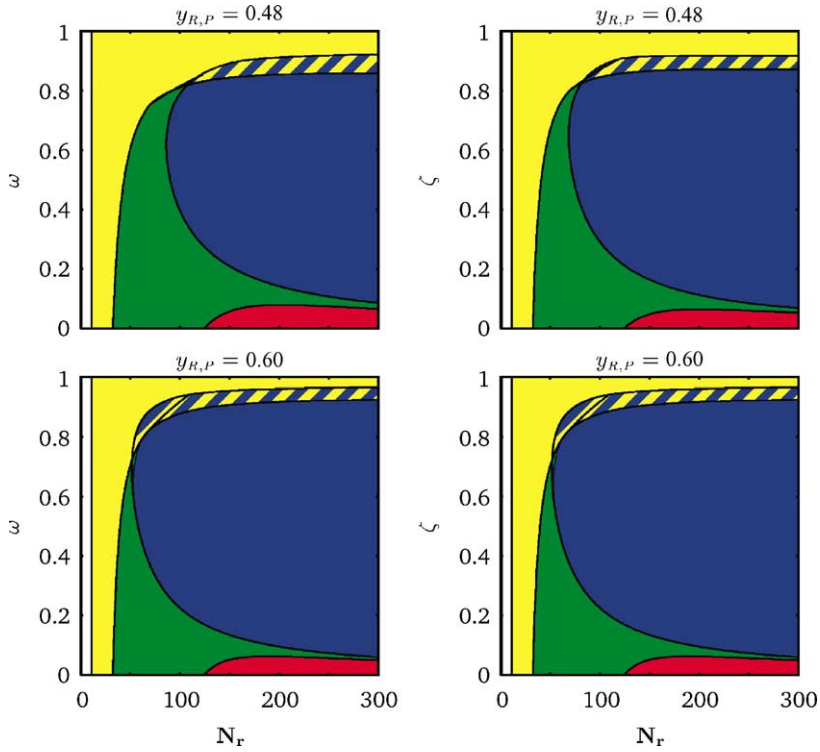

Fig. 3. Bifurcation diagrams of the timebudget model (left positions) and the trade-off model (right positions) at $y_{R,P} = 0.48, 0.60$. Different colors refer to differences in asymptotic qualitative behavior. Yellow: *N–R–C*, blue: *N–R–P*, bright green: *N–R–C–P* in equilibrium, dark-green: two attractors for *N–R–C–P* in equilibrium, red: *N–R–C–P* in non-equilibrium, dashed: two attractors of corresponding colors. Parameter values are as indicated in Table 2, $\boldsymbol{D} = 0.03$. Pure competition implies $\omega, \zeta = 1$, whereas $\omega, \zeta = 0$ corresponds to a linear food chain.

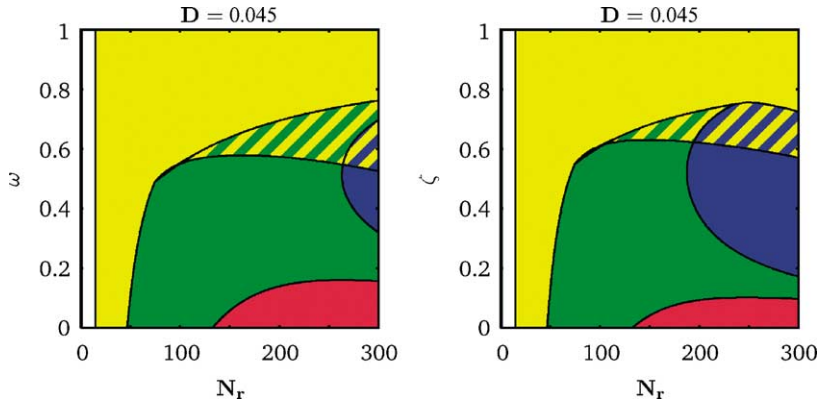

Fig. 4. Bifurcation diagrams of the timebudget model (left) and the trade-off model (right) at $\boldsymbol{D} = 0.045$ and $y_{R,P} = 0.36$. Different colors refer to differences in asymptotic qualitative behavior. Yellow: *N–R–C*, blue: *N–R–P*, bright green: *N–R–C–P* in equilibrium, dark-green: two attractors for *N–R–C–P* in equilibrium, red: *N–R–C–P* in non-equilibrium, dashed: two attractors of corresponding colors. Parameter values are as indicated in Table 2. Pure competition implies $\omega, \zeta = 1$, whereas $\omega, \zeta = 0$ corresponds to a linear food chain.

as follows:

- yellow: N–R–C;
- blue: N–R–P;
- bright green: N–R–C–P in equilibrium;
- red: N–R–C–P in non-equilibrium;
- dark green: N–R–C–P in equilibrium, two attracting states.

Some regions are yellow–blue shaded, which implies that either of two incompatible situations occur: the consumer outcompetes its predator and, at the same parameter values, the predator eliminates the consumer. This seems implausible, but it is not. In these regions, the system's endpoint is determined by the initial densities of all trophic niches, as is the case in all shaded regions. In this particular situation, neither the intraguild predator, nor the intraguild prey can invade a system in infinitesimal small numbers when the other species is already present. However, should either infest the system in sufficiently large numbers, it will start to take over and oust the other species. An example of this is shown if Fig. 5. Here, at some point in time, a number of consumers infests an oscillatory N–R–P system. In the left graph, the inroad of consumers is smaller ($3\,\mathrm{mg\,l^{-1}}$) than in the right graph ($6\,\mathrm{mg\,l^{-1}}$). The N–R–P system is resistant to invasion of the smaller inroad, but it collapses when the intrusion is as large as in the graph to the right. Note that in an oscillatory system, the success of such an infestation depends on the moment of intrusion as well.

We concentrate our analyses on three main issues. These are

- effects of the growth efficiency $y_{R,P}$ on food web dynamics;
- the dynamics of the time budget model versus the trade-off model;
- the effects of turn-over rates.

The position of the bifurcation diagrams facilitates an integrated interpretation of the modelling results is facilitated. The graphs are presented as rows of pairs, where the left diagram depicts the time budget model and the right represents the trade-off model. There is a series of such comparable graphs at four different values for $y_{R,P}$, the yield of resource biomass to omnivore biomass. When this yield is 0.60, the intraguild predator grows as efficient on producers as on consumers, i.e. $y_{R,P} = y_{C,P}$. This implies that the expressions for ω and ζ become identical (compare Eqs. (2) and (4), so that the time budget model and the trade-off model become one and the same. Therefore, the corresponding graphs of the time budget and the trade-off approach are also identical.

Finally, we present an analysis op the model at an alternative dilution rate. This parameter can be conceived of as the turn-over rate of the ecosystem.

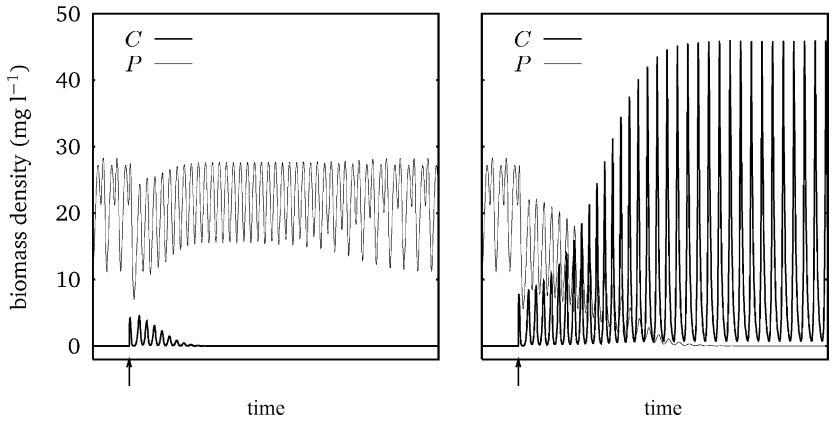

Fig. 5. Demonstration of alternative attractors at a single parameter set. In both figures, the consumer species infests a stable oscillatory producer–intraguild predator system. The moment of intrusion is marked by an arrow. In the left diagram, the inroad density ($3\,\mathrm{mg\,l^{-1}}$) is insufficient to oust the intraguild predator, which is able to recover and suppress the consumer species. In the diagram to the right, the inroad is large enough ($6\,\mathrm{mg\,l^{-1}}$) to thrive the omnivorous species to extinction. As a result, an oscillatory producer–consumer system evolves. Parameter values are $\boldsymbol{D} = 0.045$, $\boldsymbol{N_r} = 300.0$, $\zeta = 0.7$.

This property affects the dynamic behavior of food chain models considerably (Smith and Waltman, 1994; Vayenas and Pavlou, 1999b, 2001). In the description of model behavior, we compare the diagrams pairwise and at increasing yields. We first concentrate on regions in which all trophic niches can be occupied. Later, we concentrate on mutual invasibility, and we conclude with comparing regions with multiple attracting states and complex dynamics.

3.2. Coexistence of intraguild predator and intraguild prey

Regions of potential coexistence of the two highest trophic niches are colored green or shaded green and another color. At the lowest yield ($y_{R,P} = 0.24$), the regions of coexistence of the time-budget and the trade-off graphs are much alike. Still, there are some minor differences, which play a role at high nutrient levels. Firstly, there is a dark green region in which the trade-off model has two attracting equilibria with all trophic niches occupied. Secondly, there is a blue region in the trade-off model, which is not present in the time budget model. In this region the intraguild prey species can not survive the presence of intraguild predators.

When $y_{R,P} = 0.36$, the biomass conversion from R to P is just as efficient as the conversion from R via C to P. Here, both models behave as predicted by McCann and Hastings (1997), Diehl and Feißel (2000); and Mylius et al. (2001) in a large part of parameter space, i.e. at low nutrient inputs C outcompetes P, stable coexistence of C and P dominates at intermediate nutrient levels and P ousts C at high nutrient levels. The potential for coexistence is generally larger in the time budget model than in the trade-off model. Moreover, a relative low interaction strength between P and R (i.e. a low value of ω or ζ) proves to be beneficial for coexistence, which is in agreement with the results of Bondavalli and Ulanowicz (1999).

The main difference between the bifurcation diagrams concerning $y_{R,P} = 0.36$ and $y_{R,P} = 0.48, 0.60$ is that the region of potential coexistence becomes smaller. This is because the effect of increasing $y_{R,P}$ is an enhanced competitiveness of the intraguild predator, as compared to the intraguild prey.

The simulations with increased dilution rates (0.045 instead of 0.03) pertain to $y_{R,P} = 0.36$. Compared to the corresponding graphs at $\boldsymbol{D} = 0.03$, there are two major differences. Firstly, stable coexistence of C and P at the higher dilution rate is bound to somewhat lower values of the interaction parameters ω and ζ. This implies that higher turnover rates favors predatory omnivores rather than competitive omnivores. Second, at the higher dilution rate the blue area, in which C cannot persist in the presence of P, originates at higher levels of enrichment. This is because the diminution of P due to enhanced dilution relaxes the predation pressure on C.

3.3. Invasibility

The intraguild prey, C, may invade in all regions that do not contain blue, whereas the intraguild predator, P, can invade in all regions without yellow. An increase in $y_{R,P}$ is always beneficial to P, so that such an increment enlarges the parameter region in which P can invade. Effectively, an increase in $y_{R,P}$ strengthens the interaction between R and P. The intraguild prey will not benefit from an increase in $y_{R,P}$. As a consequence, it will lose competitiveness. The regions of mutual invasibility and persistence of the intraguild configuration become smaller with increasing interaction strengths between P and R, which is in accordance with Bondavalli and Ulanowicz (1999).

In general, P cannot invade if the nutrient provision is too low. This is a consequence of the assumption that C is a better competitor for the common resource than P. The effect of this superior competitiveness increases with increasing ω or ζ.

The region in which C can invade is generally smaller in the trade-off simulations than in the time budget analyses. This is because the trade-off strategy involves a weighing of catching efforts of P on R against the yield. When $y_{R,P}$ is lower than $y_{C,P}$, the trade-off strategy imposes a higher competitiveness on P than the time budget strategy. This is because a reduction in predation ability on C results in a non-symmetrically increased catching efficiency on R; in the time budget strategy this balance is symmetric.

In line with the predictions of Bondavalli and Ulanowicz (1999), both strategies predict mutual invasibility (the unpatterned green regions) to be most likely at low interaction strengths between P and R, where both species can invade at the relative largest

range of nutrient supply densities. This effect is most pronounced in the trade-off strategy.

An increased dilution rate brings about two marked effects. Firstly, the region of mutual invasibility generally covers a larger range of nutrient enrichment levels. Secondly, mutual invasibility is restricted to a smaller range of the interaction parameters. This result might be used as an indication that systems at high turn-over rates are less sensitive to nutrient enrichment.

3.4. Complex dynamics and multiple stable states

The red regions in the bifurcation diagrams correspond to parameter values, where the system's attracting state is not an equilibrium. All diagrams show such dynamics at high nutrient enrichment levels and at values of ω and ζ where the system approximates a food chain. This phenomenon has been widely used to demonstrate the 'paradox of enrichment' in food chains (Abrams and Roth, 1994; Boer et al., 1998). Bifurcation analyses reveal that red regions in the right bottom positions of the diagrams comprise chaos as a result of a cascade of period doublings (unpublished data, cf. Boer et al., 1998; Kooi et al., 1998, 2002). These red regions vanish rapidly when the interaction parameter changes to more competitive behavior of P. This result corroborates the current view that weak interactions stabilize food webs (Huxel and McCann, 1998; McCann and Hastings, 1997). This effect is stronger in the trade-off strategy than in the time budget strategy. This may indicate that ecological trade-off strategies can reduce complex dynamics in food webs.

At low values of $y_{R,P}$ there is a second complex region in the diagrams, placed at much higher values of the interaction parameter (± 0.7), although bifurcation analyses revealed that these particular regions do not contain chaotic dynamics. The combination of a relatively competitive P with a low yield on the common resource may give rise to complexity. This effect is more pronounced in the trade-off strategy.

All bifurcation diagrams have regions with multiple attracting states. Alternative stable endpoints arise from tangent bifurcations and hold the potential for hysteresis loops. These loops have been demonstrated in a variety of natural ecosystems (Scheffer et al., 2001). In our models, the multiple attracting states usually correspond to relatively large values for the interaction parameter. In general, the regions involved mark the transition from regions where P is outcompeted by C on the one side and regions where the three-trophic system persists or where P ousts C on the other side.

In the time budget model at $y_{R,P} = 0.24, 0.36$ and the trade-off model at $y_{R,P} = 0.36$, $\boldsymbol{D} = 0.045$, the yellow–green dashed regions mark parameter values at which both the N–R–C–P and the N–R–C assemblages attract. In these regions, loss of the intraguild predator would cause the system to shift towards a state in which it cannot re-invade.

In the trade-off model at $y_{R,P} = 0.24$, there are two attracting states in which all trophic niches are occupied at high nutrient enrichment levels and $\zeta = \pm 0.06$. Here, a catastrophic event may cause a permanent change in biomass distributions in the system, but there is no extinction of species. The persistent web is bi-stable at this set of parameters.

In all graphs where $y_{R,P} > 0.24$, there exists a yellow–blue dashed region. In these regions both the N–R–C and the N–R–P assemblages are structurally stable. Both assemblages are resistant to invasion. Should, however, the system be infested by large numbers of the non-resident species, the system undergoes a drastic change, after which the infesting species replaces the resident species.

The model simulations at $\boldsymbol{D} = 0.045$ yield larger regions of multiple stable states. This indicates that high turn-over rates might promote the occurrence of hysteresis loops in ecosystems. This result emerges from both the time budget and the trade-off model.

4. Discussion and conclusions

Our study concentrated on the influence of nutrient enrichment in an ecosystem with intraguild predation. We used two strategies for modelling the intraguild predation interaction, including a time budget assumption and an efficiency trade-off for the omnivore's foraging behavior.

The predictions of both modelling approaches are similar for the largest part of the explored parameter space. However, the models may behave different at interaction parameter values roughly between $0.6 < \omega, \zeta < 0.8$. So, far, this parameter range has received little theoretical attention, as McCann and

Hastings (1997) were primarily interested in the parameter range $0 < \omega < 0.5$. However, Navarette et al. (2000) showed that this more competitive type of intraguild predation can play a dominant role in natural ecosystems. Our analyses show that intraguild predation close to competition yields a rich repertoire of ecologically plausible dynamic behaviors.

Our results are consistent with the findings of Huxel and McCann (1998), Boer et al. (2001) and Persson et al. (2001) in that the models predict the paradox of enrichment for food chains, i.e. complex behavior occurs at high nutrient inlet densities. However, this complex behavior is readily eliminated when a weak interaction between the intraguild predator and the resource species is established. Therefore, our results support the view that weak interactions promote stability and persistence of food webs (Paine, 1992; Polis, 1998; McCann et al., 1998; Bondavalli and Ulanowicz, 1999; Borrvall et al., 2000; Post et al., 2000; McCann, 2000; Fussman and Heber, 2002). We find this phenomenon to be more demonstrative in the trade-off model than in the time budget model. Under the assumption that the trade-off approach adds realism, our results further substantiate the current view. If complex dynamics, as often found in theoretical food chain studies, are so easily eliminated by weak interactions, and intraguild predation in natural ecosystems is widespread, the predicted complex dynamics might be artefactual, rather than realistic.

Mylius et al. (2001) find that coexistence of P and C requires a relatively low attack rate of P on R. In general terms, such behavior corresponds to low values of interaction parameters ω, ζ. Our results corroborate this finding to a large extent, as we find the largest regions of coexistence in the lower parts of the bifurcation diagrams. In addition, we find that both the yield $y_{R,P}$ and dilution rate $\boldsymbol{D}$ are important modifiers in determining the scope of potential coexistence of C and P.

We find that intraguild predation in the vicinity of exploitative competition ($\zeta, \omega \rightarrow 1$) results in extinction of the intraguild predator. This result is in agreement with the competitive exclusion principle. However, at somewhat lower values for ω or ζ, the existence of multiple stable states in which both the N–R–C system as the N–R–P system are resistant to invasion, is a common phenomenon in our analyses. Both endpoints are equivalent in the sense that both C and P figure as consumer guilds. According to Tilman's R^*-rule (Tilman, 1990), the better competitor will always oust his opponent. In our models the consumer is the better competitor for the resource species. Resistance of the N–R–P system to invasion of C suggests that a weak interaction between P and C can be a good defence mechanism for inferior competitors.

At high nutrient enrichment levels and intermediate interaction strengths between P and R our model predicts exclusion of C. This finding corresponds with current theory (Holt and Polis, 1997; McCann and Hastings, 1997; Diehl and Feißel, 2000, 2001). This effect depends on the intraguild predator's growth efficiency on the resource species. Moreover, it acts more dominantly in the trade-off model than in the time budget model. It appears that a modestly competitive intraguild predator bearing a low yield on the common resource, in combination with a low system turn-over rate provides the best environment for a persistent food web with omnivory.

As a final result, our model predicts regions of multiple attracting in all of the simulations. At $\boldsymbol{D} = 0.045$, the corresponding regions contribute significantly to the overall dynamics. The regions involved cover a transition trajectory between two extremes, for instance at the one end of the region P goes extinct, whereas at the other end C is eliminated. The existence of multiple stable states in natural systems has received increasing interest in the past years (Scheffer et al., 2001), and an increasing amount of cases have been reported. If omnivory is a potential cause for the emergence of multiple stable states, and it is widespread in natural systems, it might be one of the explanations for the ubiquitousness of multiple stable states.

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