MATHEMATICAL BIOSCIENCES
AND ENGINEERING
Volume **5**, Number **3**, July **2008**

http://www.mbejournal.org/

pp. **567–583**

STABILIZATION DUE TO PREDATOR INTERFERENCE: COMPARISON OF DIFFERENT ANALYSIS APPROACHES.

G.A.K. van Voorn

Dept. Theor. Biology, Vrije Universiteit
de Boelelaan 1087, 1081 HV Amsterdam, the Netherlands

D. Stiefs

ICBM, Carl von Ossietzky Universität
PF 2503, 26111 Oldenburg, Germany

T. Gross

Dept. of Chem. Eng., Princeton University,
Engineering Quadrangle, Princeton, NJ 08540, USA

B.W. Kooi

Dept. Theor. Biology, Vrije Universiteit
de Boelelaan 1087, 1081 HV Amsterdam, the Netherlands

U. Feudel

ICBM, Carl von Ossietzky Universität
PF 2503, 26111 Oldenburg, Germany

S.A.L.M. Kooijman

Dept. Theor. Biology, Vrije Universiteit
de Boelelaan 1087, 1081 HV Amsterdam, the Netherlands

(Communicated by Yang Kuang)

Abstract. We study the influence of the particular form of the functional response in two-dimensional predator-prey models with respect to the stability of the nontrivial equilibrium. This equilibrium is stable between its appearance at a transcritical bifurcation and its destabilization at a Hopf bifurcation, giving rise to periodic behavior. Based on local bifurcation analysis, we introduce a classification of stabilizing effects. The classical Rosenzweig-MacArthur model can be classified as weakly stabilizing, undergoing the paradox of enrichment, while the well known Beddington-DeAngelis model can be classified as strongly stabilizing. Under certain conditions we obtain a complete stabilization, resulting in an avoidance of limit cycles. Both models, in their conventional formulation, are compared to a generalized, steady-state independent two-dimensional version of these models, based on a previously developed normalization method. We show explicitly how conventional and generalized models are related and how to interpret the results from the rather abstract stability analysis of generalized models.

2000 *Mathematics Subject Classification.* Primary: 92D25; Secondary: none.

Key words and phrases. bifurcation analysis, functional response, generalized model, stability.

GVV is supported by the Netherlands Organization for Scientific Research (NWO-CLS) grant no. 635,100,013. TG thanks the Alexander von Humboldt Foundation for financial support.

1. **Introduction.**

One central issue in the field of theoretical ecology deals with the stability properties of ecosystems. Since the observation that several classical ODE food chain models, such as the Rosenzweig–MacArthur model [33], display oscillatory dynamics after a significant increase in the value of parameters associated with enrichment [20, 32, 9], an enormous literature has amounted regarding this subject.

Although the paradox is now deemed an artifact, it has been concluded there must be stabilizing mechanisms functioning in the currently existing ecosystems [38]. A very large number of such mechanisms or factors have been proposed, which, ironically, all more or less seem to claim general applicability, although it is much more likely that they all attribute to some degree under different circumstances. Some of these are age or size structure in the predator or prey population [17, 18]; anti-predator behavior of the prey [28]; spatial heterogeneity [21, 36, 29]; self-limitation of the prey [22]; nonlinear mortality of the predator [3]; stoichiometric food supply constraints [27]; maturation delays [10]. Observe, however, that some of these mechanisms can also have the opposite effect (destabilization), depending on the strength of the mechanism. See also [34] for a recent review on stabilizing factors in simple predator–prey food chain models.

Many of the (de)stabilizing mechanisms involve manipulation of the functional response. The functional response describes the predation rate as a function of the abundances of predator and prey. One of the most commonly used functional responses is the Holling type-II functional response [19], which is exclusively prey-dependent. However, several of the alternative functional response formulations are also predator-dependent or not exclusively prey-dependent. Some formulations involve the inclusion of nonstandard prey populations, among them inedible populations [25, 8], invulnerable prey [1], decoy species [41], and inducibly defended prey [39]. In [23], predator cannibalism was incorporated, which modifies the functional response. Predator intraspecific interference has been included in a functional response by many authors, e.g. [4, 6, 35], and it has been shown that such functional responses with predator interference included can even dampen the oscillations in medium-sized food webs [30].

Another approach to analyzing the influence of the exact mathematical formulation of the functional response is the use of generalized models, in which the functional response is not a priori specified [14, 15, 13]. This method allows the investigation of the stability properties of nontrivial equilibrium states in a very general form and enables one to conclude that any biological effect that changes the form of the functional response at least slightly can potentially have a large impact on the stability of the system. As such, the stability of ecological systems is extremely sensitive to the exact form of the functional response [14, 7].

One point of criticism raised with regard to the use of the term *stability* in biological papers must be mentioned. Grimm and Wissel [11] made an extensive list summarizing 163 definitions of 70 different stability concepts. They concluded that “the general term ‘stability’ is so ambiguous as to be useless.” Rinaldi and Gragnani [31] made related observations, stating that the validity of robust conclusions regarding (de)stabilizing factors in data analysis or simulations is highly questionable. Throughout this paper we use the mathematical definition of stability of steady states with respect to small perturbations [16, 37]).

Here we study the classical two-level food chain model from [33] (abbreviated RM) with the default Holling type-II functional response [19] and compare it with the Beddington–DeAngelis functional response [4, 6] (abbreviated BD). We analyze these models using two different approaches. On the one hand we perform a classical stability analysis, and on the other hand we represent both models in terms of generalized predator-prey model formulations to compare both approaches. In conventional model formulations it is difficult to study how the choice of one specific functional form affects the stability, since any variation of a function will in general cause a variation of the equilibrium values and will therefore affect all other processes in the model as well. Hence, one cannot distinguish between direct and indirect effects. By contrast, in generalized model formulations the stabilizing or destabilizing effect is captured by generalized parameters, independent of the equilibrium values. However, since generalized models and their analysis are rather abstract, we show here explicitly how both approaches are related to each other and how to interpret the results of such a generalized investigation. Both stability analyses yield a classification of stabilizing effects resulting in weak, strong, or complete stabilization.

The models are analyzed using local bifurcation analysis. Several types of bifurcation points can be interpreted in an ecological way [24]. The Hopf bifurcation is generally interpreted as a point of destabilization, while the fold bifurcation is generally associated with persistence, especially the transcritical bifurcation [5]. In light of the debate regarding the use of the term stability, our stability classification specifically compares the point of destabilization (the location of the Hopf bifurcation) with the persistence boundary (the location of the transcritical bifurcation), where the two studied models (RM and BD) function as example cases.

The paper is organized as follows. In Section 2 we discuss the definition of stability and the local bifurcation types involved, after which in Subsection 2.2 the stability properties of the RM and the BD models in a conventional formulation are discussed. In Section 3 we introduce an adapted version of the generalized predator-prey model by [14], and we define the generalized parameters. In Section 4 we specify the generalized parameters for the RM and BD models and give the local bifurcation analyses of these models. Also, we discuss the stability properties of the generalized model formulations. Finally, in Section 5 we put the results in a broader context.

2. **Bifurcation analysis.**

For the analysis of our models we introduce three types of stabilization, based on local bifurcation analysis and limited to a two-dimensional setting. Stability itself is defined as the local linear asymptotic stability of an equilibrium, also called a steady state. Taking a two-dimensional system of ODE's

$$\dot{X}_1 = F_1(X_1, X_2)\ , \tag{1a}$$

$$\dot{X}_2 = X_2 F_2(X_1, X_2, p)\ , \tag{1b}$$

the stability of an equilibrium (X_1^*, X_2^*) of this system can be determined by evaluating the eigenvalues of the Jacobian matrix

$$\mathbf{J} = \begin{pmatrix} J_{11} & J_{12} \\ J_{21} & J_{22} \end{pmatrix}\Bigg|_{X_1=X_1^*, X_2=X_2^*}\ , \tag{2}$$

where

$$J_{11} = \frac{\partial F_1(X_1, X_2)}{\partial X_1}\ ,\ J_{12} = \frac{\partial F_1(X_1, X_2)}{\partial X_2}\ ,\ J_{21} = X_2^* \frac{\partial F_2(X_1, X_2)}{\partial X_1}\ ,$$
$$J_{22} = X_2^* \frac{\partial F_2(X_1, X_2)}{\partial X_2} + F_2(X_1^*, X_2^*)\ .$$

This definition applies only to an individual equilibrium. A stable equilibrium corresponding to the situation in which all eigenvalues have negative real parts refers to a locally attracting node or spiral, while an unstable equilibrium where at least one real eigenvalue is positive or a conjugate complex pair of eigenvalues has positive real parts can be a locally repelling node or spiral or a saddle equilibrium.

2.1. **Bifurcation points.**

In bifurcation analysis the stability of separate equilibria is monitored under smooth, continuous parameter variation. A change in stability of an equilibrium at a specific parameter value indicates a bifurcation point (for more information, see [16, 40, 26], and for the applications in ecological models [3, 24]). For the classification two bifurcation types are of importance: the transcritical and the Hopf bifurcation. Two expressions can be derived from the Jacobian matrix equation (2) that are useful in localizing these bifurcations, and that we use in the stability classification, namely

$$det(\mathbf{J}) = J_{11}J_{22} - J_{12}J_{21} = 0\ , \tag{3a}$$
$$tr(\mathbf{J}) = J_{11} + J_{22} = 0\ , \tag{3b}$$

which are the determinant and the trace of the Jacobian matrix, respectively.

Transcritical bifurcation. A fold bifurcation occurs at a specific parameter value where one real eigenvalue is zero. When two equilibria $\mathbf{X}^*, \tilde{\mathbf{X}}$ merge to form a saddle-node equilibrium, this is a saddle-node or tangent bifurcation. The transcritical bifurcation (TC) is a degenerate type of fold bifurcation that occurs for

$$F_2(\tilde{X}_1, \tilde{X}_2, p_{TC}) = 0\,, \tag{4}$$

where $\tilde{X}_2 = 0$. The transcritical bifurcation is also defined by $det(\mathbf{J}) = 0$.

The TC can biologically be interpreted as an existence boundary for a species, given it occurs at a zero biomass equilibrium for this species [24]. In the specific ecological models meant in this paper the equilibrium $\tilde{X}_2 = 0$ is stable for $p < p_{TC}$ and becomes unstable at p_{TC}. The stability then is taken over by an invading equilibrium $\mathbf{X}^*$ in the region $p > p_{TC}$, which means there is a stable positive biomass X_2^*. We refer to this latter condition as *persistence*.

Hopf bifurcation. The second type of bifurcation we consider is the Hopf bifurcation, denoted H. Such a bifurcation occurs when the real part of a complex pair of eigenvalues becomes zero. At the Hopf bifurcation the involved equilibrium switches from stable to unstable (or vice versa). The criterion for the Hopf bifurcation is met when the trace equals zero, while the determinant is positive. The arising limit cycle can be either stable (supercritical Hopf) or unstable (subcritical Hopf). The models considered here exhibit a supercritical Hopf bifurcation, where a stable limit cycle attractor is born that gives rise to periodic behavior.

The transition from a stable equilibrium to stable periodic behavior is often connected to destabilization, as meant in [32]. Under enrichment of a predator-prey system first a Hopf bifurcation occurs, and after further enrichment the periodic cycle tends to increase in size until stochastic extinction becomes very likely.

2.2. **Stability in the RM and BD models.** Both the RM and the BD models have logistic growth of the prey X_1 and linear mortality R of the predator X_2, written as

$$\frac{dX_1}{dt} = rX_1\big(1 - \frac{X_1}{K}\big) - G(X_1, X_2)X_2 \ , \tag{5a}$$

$$\frac{dX_2}{dt} = \kappa G(X_1, X_2)X_2 - RX_2 \ , \tag{5b}$$

where κ is the yield or efficiency, the ratio between ingested biomass X_1 and the production of biomass X_2 from it, which is taken smaller than 1 and assumed to be constant. The scaled functional response, denoted $G(X_1, X_2)$, is in the RM model the standard Holling type-II functional response

$$G(X_1) = \frac{X_1}{T_S + T_H X_1} \ , \tag{6}$$

where T_S is the searching time and T_H is the handling time per prey item. Both these parameters can be rewritten as given in Table 1, which will give more insight further on. The BD model has a Beddington–DeAngelis functional response [6], written as

$$G(X_1, X_2) = \frac{X_1}{T_S + T_H X_1 + T_I X_2} \ , \tag{7}$$

which includes mutual interference of the predator individuals, with interaction time T_I per predator individual.

The location of the two above-mentioned bifurcations, the transcritical bifurcation TC as the existence boundary of the positive equilibrium X_2^*, and the Hopf bifurcation H, corresponding to the destabilization of X_2^*, determines the stability interval in parameter space. In particular, the distance between TC and H is the crucial quantity to be estimated. As such, by comparison of the curves of the Hopf bifurcation and the transcritical bifurcation in two-parameter space, where one parameter is the enrichment parameter K and the other is the mortality rate R, we can define two types of stabilization occurring in a model. Figure 1 gives the two possible scenarios.

Continuation in K and, for instance, R in the RM model results in *weak* stabilization, as shown in Figure 1, upper panel. The stable region of the unique positive equilibrium can be described purely algebraically, using the trace and determinant of the Jacobian matrix. After substitution in Equation (4, 3b) we get

$$K_{TC}^{RM} = \frac{RC}{\mu - R} \ , \tag{8a}$$

$$K_{H}^{RM} = \frac{C(R+\mu)}{\mu - R} = K_{TC} + \frac{\mu C}{\mu - R} \ . \tag{8b}$$

With increasing R towards μ the interval $|K_{TC}^{RM} - K_{H}^{RM}|$ becomes infinite. Calculation of the asymptotes of the two bifurcations for R, called R_{TC}^{RM} and R_{H}^{RM}, with $K \to \infty$, yields

$$\lim_{K\to\infty} R_{TC}^{RM} = \lim_{K\to\infty} R_{H}^{RM} = \mu \ . \tag{9}$$

In other words, the interval $|R_{TC}^{RM} - R_H^{RM}| \to 0$ for increasing K; hence we term that behavior weak stabilization.

In the BD model with mutual predator interference continuation in the same parameters K and R results in *strong* stabilization, as shown in Figure 1, lower panel. The same limit case analysis as in the RM model gives

$$K_{TC}^{BD} = \frac{RC}{\mu - R} , \tag{10a}$$

$$K_H^{BD} = \frac{C(RT_I\mu - \mu - R)^2}{(T_I\mu - 1)(\mu^2(rT_I + RT_I - 1) + R^2(1 - T_I\mu))} , \tag{10b}$$

where we assume that the time spent on an interaction $T_I > 0$. Intraspecific interactions do not play a role at the transcritical bifurcation since $\tilde{X}_2 = 0$, so $K_{TC}^{BD} = K_{TC}^{RM}$ and also $\lim_{K\to\infty} R_{TC}^{BD} = \lim_{K\to\infty} R_{TC}^{RM} = \mu$. Calculation of $\lim_{K\to\infty} R_H^{BD}$ results in a rather lengthy expression, which is not given here, but there is a finite range $\lim_{K\to\infty} R_{TC}^{BD} < R < \lim_{K\to\infty} R_H^{BD}$ where the system has a stable positive equilibrium for all values of K. This means that the distance $|R_{TC}^{BD} - R_H^{BD}|$ remains finite for all K as denoted by the arrow A in Figure 1. As a consequence, the distance $|K_{TC}^{BD} - K_H^{BD}|$, which is rather small for small R (arrow B), becomes infinite for all R between $\lim_{K\to\infty} R_{TC}^{BD}$ and $\lim_{K\to\infty} R_H^{BD}$ (arrow C). Within this rather large interval of R the Hopf bifurcation as the existence boundary of stable steady state is avoided leading to *strong* stabilization.

If we consider the variation of a third parameter, namely the interaction time T_I, we can observe an additional effect. The size of the interval of R where the Hopf bifurcation is avoided depends on T_I. By increasing the value of T_I it is possible to avoid the Hopf bifurcation in the whole range of $0 < R < \mu$ and for all $K > 0$. Rewriting the lengthy expression for $\lim_{K\to\infty} R_H^{BD}$ with respect to T_I, the minimal value of T_I required for *complete* avoidance of the Hopf bifurcation is given as

$$\tilde{T}_I = \lim_{K\to\infty} T_{I,H} = \frac{\mu^2 - R^2}{\mu(\mu(r + R) - R^2)} , \tag{11}$$

where $0 < R < \mu$, i.e., for $T_I > \tilde{T}_I$ destabilization does not occur for any K. We call this effect *complete* stabilization.

Strong stabilization was shown earlier by Vos et al. [39], who considered a two-parameter bifurcation diagram displaying both the transcritical and the Hopf bifurcation curves for a model with a predator and a prey species with two subpopulations, one defensible and one indefensible. A similar type of stabilization was shown by Kretzschmar et al. [25] (Fig. 5), although there the intrinsic growth rate r was considered as the enrichment parameter.

3. Generalized model formulation.

It is difficult to compare models with different terms of interaction, since each change in the functional form would also affect the value of the steady state. To draw more general conclusions on stabilization effects in models, we use generalized parameters, adapted from those as described in [14]. Such generalized models allow to analyze specific equilibrium-independent effects.

In the generalized approach we do not specify the response function $G(X_1, X_2)$ in Equation (5). Furthermore, we assume that there are (at least) two equilibria, one positive steady state denoted by $\mathbf{X}^* = (X_1^*, X_2^*)$, and one zero equilibrium denoted by $\tilde{\mathbf{X}} = (X_1^*, 0)$.

It is important to mention that the following consideration of the generalized models differs from the one introduced in [14] in the sense that here it has been explicitly taken into account that the functional response is at least linear in the predator, so that it can be written as $G(X_1, X_2)X_2$. This particular form can be regarded as a restriction or loss of generality compared to [14], but it is necessary to distinguish between the positive and the zero equilibrium. In the following we make use of this distinction. Furthermore, we note that we do not aim at a stability analysis of the generalized models in their whole generality but rather to show how one can relate generalized models to conventional models. This is a nontrivial task since there is no one-to-one correspondence between generalized parameters, describing the shape of the functional response and parameters in conventional models. Nevertheless it is possible to find and explore this relationship as we show next.

3.1. **The positive equilibrium.** To substitute the unknown equilibrium $\mathbf{X}^*$ we introduce the normalized variables

$$x_i = \frac{X_i}{X_i^*} \ , \tag{12}$$

with $i = 1, 2$ and the normalized functions

$$g(x_1, x_2) = \frac{G(X_1^* x_1, X_2^* x_2)}{G(X_1^*, X_2^*)} \ . \tag{13a}$$

After substitution into Equation (5) we get the equations

$$X_1^* \frac{dx_1}{dt} = rX_1^* x_1 - g(x_1, x_2) G(X_1^*, X_2^*) X_2^* x_2 - \frac{rX_1^{*2}}{K} x_1^2 \ , \tag{14a}$$

$$X_2^* \frac{dx_2}{dt} = \kappa g(x_1, x_2) G(X_1^*, X_2^*) X_2^* x_2 - R X_2^* x_2 \ . \tag{14b}$$

Because of normalization, the system now has a positive equilibrium $x_i^* = 1$, $i = 1, 2$ and for the function $g(x_1, x_2)$ holds $g(x_1^*, x_2^*) = 1$, which is the strong point of the generalization method. Observing the above equations in the equilibrium results in the following expressions for time scales at both levels x_i

$$\alpha_1 := r = \frac{G(X_1^*, X_2^*) X_2^*}{X_1^*} + \frac{rX_1^*}{K} \ , \tag{15a}$$

$$\alpha_2 := R = \kappa G(X_1^*, X_2^*) \ . \tag{15b}$$

Additional scaling parameters can be defined

$$m := \frac{X_1^*}{K} \ , \tag{16a}$$

$$n := 1 - m = \frac{G(X_1^*, X_2^*) X_2^*}{\alpha_1 X_1^*} \ , \tag{16b}$$

where n and m represent the relative importance of the predatory and non-predatory loss terms, respectively. We can now rewrite Equation (5) in the normalized system

$$\frac{dx_1}{dt} = \alpha_1\bigl(x_1 - ng(x_1,x_2)x_2 - mx_1^2\bigr) \ , \tag{17a}$$

$$\frac{dx_2}{dt} = \alpha_2 x_2\bigl(g(x_1,x_2) - 1\bigr) \ . \tag{17b}$$

3.2. **The zero equilibrium.** To deal with a zero equilibrium $\tilde{\mathbf{X}}$, it is not possible to use the normalized variable $x_2 = X_2/\tilde{X}_2$ since $\tilde{X}_2 = 0$. Instead, we use

$$x_1 = \frac{X_1}{\tilde{X}_1} \ , \ x_2 = X_2 \ . \tag{18}$$

Note that this is not a strict normalization, because the variable x_2 is not dimensionless. The following normalized functions are redefined accordingly:

$$\tilde{g}(x_1,x_2) = \frac{G(\tilde{X}_1 x_1, x_2)}{G(\tilde{X}_1, 0)} \ . \tag{19}$$

After substitution into Equation (5) we have the ODE's

$$\tilde{X}_1\frac{dx_1}{dt} = r\tilde{X}_1 x_1 - \tilde{g}(x_1,x_2)G(\tilde{X}_1,0)x_2 - \frac{r\tilde{X}_1^2}{K}x_1^2 \ , \tag{20a}$$

$$\frac{dx_2}{dt} = \kappa\tilde{g}(x_1,x_2)G(\tilde{X}_1,0)x_2 - Rx_2 \ . \tag{20b}$$

Based on these equations, some of the scaling parameters differ from those defined in the previous subsection. Considering Equation (20a) in the zero equilibrium yields $\alpha_1 = r = r\tilde{X}_1/K$ and therefore $\tilde{X}_1/K = 1$. By defining

$$\alpha_{21} := \kappa G(\tilde{X}_1, 0) \ , \tag{21a}$$

$$\alpha_{22} := R \ , \tag{21b}$$

$$\tilde{n} := \frac{G(\tilde{X}_1,0)}{\alpha_1}\tilde{X}_1 \ , \tag{21c}$$

we can now rewrite Equation (5) as

$$\frac{dx_1}{dt} = \alpha_1\bigl(x_1 - \tilde{n}\tilde{g}(x_1,x_2)x_2 - x_1^2\bigr) \ , \tag{22a}$$

$$\frac{dx_2}{dt} = x_2\bigl(\alpha_{21}\tilde{g}(x_1,x_2) - \alpha_{22}\bigr) \ . \tag{22b}$$

Note that in general $\alpha_{21} \neq \alpha_{22}$ in case of a zero equilibrium.

3.3. **Generalized parameters.** We can define generalized parameters for the generalized model formulation that can function as bifurcation parameters. The advantage of generalized parameters is that they describe generic, rather than specific, properties of the model.

We define the following generalized parameters, adapted from [14]:

$$\gamma_i = \left.\frac{\partial g(x_1,x_2)}{\partial x_i}\right|_{x=x^*} \ , \tag{23}$$

Table 1. List of parameters used in the RM/BD models. For the bifurcation parameters a range has been given.

symbol	value	meaning
K	$[0, \infty\rangle$	carrying capacity
r	0.5	prey specific growth rate
μ	0.2	predator specific growth rate
κ	0.4	yield; conversion coefficient
C	9.	saturation constant
$T_S = C\kappa/\mu$	18.	searching time
$T_H = \kappa/\mu$	2.	handling time
R	$\langle 0, \mu]$	natural mortality
T_I	$[0, \infty\rangle$	interaction time per predator

where $i = 1, 2$. Parameter γ_1 reflects the dependence of the predator on the prey, where $\gamma_1 \to 0$ for abundant prey, while larger values of γ_1 are interpreted as prey scarcity. Parameter γ_2 denotes the predator sensitivity with respect to the predator species. For $\gamma_2 = 0$ (the RM model) there are no predator mutual interference effects, while for $\gamma_2 < 0$ (the BD model) there are mutual interference effects.

3.4. **Generalized stability criteria.**

The Jacobian matrix for the two-dimensional normalized model at the positive equilibrium is

$$\mathbf{J} = \begin{pmatrix} -\alpha_1(1 + n(\gamma_1 - 2)) & -\alpha_1 n(\gamma_2 + 1) \\ \alpha_2\gamma_1 & \alpha_2\gamma_2 \end{pmatrix} . \tag{24}$$

Observe that $x_1^* = x_2^* = g(x_1^*, x_2^*) = 1$. The condition for the Hopf bifurcation in a generalized form then is given as

$$tr(\mathbf{J}) = -\alpha_1(1 + n(\gamma_1 - 2)) + \alpha_2\gamma_2 = 0 , \tag{25}$$

and $det(\mathbf{J}) > 0$.

The condition for a transcritical bifurcation is given by the determinant of the Jacobian. In case of a positive equilibrium we would get

$$det(\mathbf{J}) = \alpha_1\alpha_2(n\gamma_1 + \gamma_2(2n - 1)) = 0 . \tag{26}$$

However, since we are interested in the transcritical bifurcation where the positive equilibrium intersects with the zero equilibrium, we can also consider the determinant of the Jacobian of the zero equilibrium.

The Jacobian evaluated at the zero equilibrium is

$$\mathbf{J} = \begin{pmatrix} -\alpha_1 & -\alpha_1\tilde{n} \\ 0 & \alpha_{21} - \alpha_{22} \end{pmatrix} . \tag{27}$$

The condition for the transcritical bifurcation is then given by

$$det(\mathbf{J}) = -\alpha_1(\alpha_{21} - \alpha_{22}) = 0 . \tag{28}$$

Thus, in the case of a transcritical bifurcation we have $\alpha_{21} = \alpha_{22}$.

4. **Model analyses.**

In this section we want to discuss the local bifurcation analyses obtained for the generalized model formulations in terms of the RM and BD model, and how results from the conventional model formulations correspond to them. This is not trivial, since the functions describing the relationship between the generalized and the conventional parameter sets are not invertible.

4.1. **Generalized parameter expressions.**

We denote the conventional parameter space as $P = \{R, K, r, \mu, \kappa, C, T_I\}$ for the used models (recall that T_S and T_H are not independent, but they depend on μ, κ and C), with the default parameter values given by Table 1. We distinguish between environmental parameters (K and R), that can easily be manipulated by an experimenter, and vital parameters, that are based on physiological processes of the species and their trophic interactions and describe the biotic system. We primarily vary the environmental parameters in the conventional bifurcation analyses, and the parameter T_I, that is considered to be the factor related to the effects on the ecosystem functioning as defined in [31].

For comparison of the results between the generalized and the conventional model formulations we analyze how the scaling and the generalized parameters, given in Equations (15, 16, 23), affect each other if we assume the functional response of that of the BD model (given in Eq. (7); it is the RM model for $T_1 = 0$). We find that

$$\gamma_1 = 1 - T_H G(X_1^*, X_2^*) = 1 - \frac{\alpha_2}{\mu} \;, \tag{29a}$$

$$\gamma_2 = -\frac{T_I X_2^*}{X_1^*} G(X_1^*, X_2^*) \;, \tag{29b}$$

where μ by default is a constant since it is a vital parameter. Please recall that the scaling parameters defined in Equations (15, 16) are related to the conventional parameters by

$$\alpha_1 = r \;, \tag{30a}$$

$$\alpha_2 = R \;, \tag{30b}$$

$$m = \frac{X_1^*}{K} \;, \tag{30c}$$

$$n = 1 - m \;. \tag{30d}$$

Hence, the bifurcation analyses of the RM and BD model in the generalized formulation use only two (α_2, m) or three (α_2, m, γ_2) parameters, respectively.

Note that we give up the generality to obtain Equation (29). In the case of the functional response of the BD model Equation (7), we have $0 < \gamma_1 < 1$ and $-1 < \gamma_2 < 0$. Adding Equation (29) we get

$$\gamma_1 + \gamma_2 = \frac{T_S}{T_S + T_H X_1^* + T_I X_2^*} \;, \tag{31}$$

and therefore $\gamma_1 + \gamma_2 > 0$ or $\gamma_1/\gamma_2 < -1$.

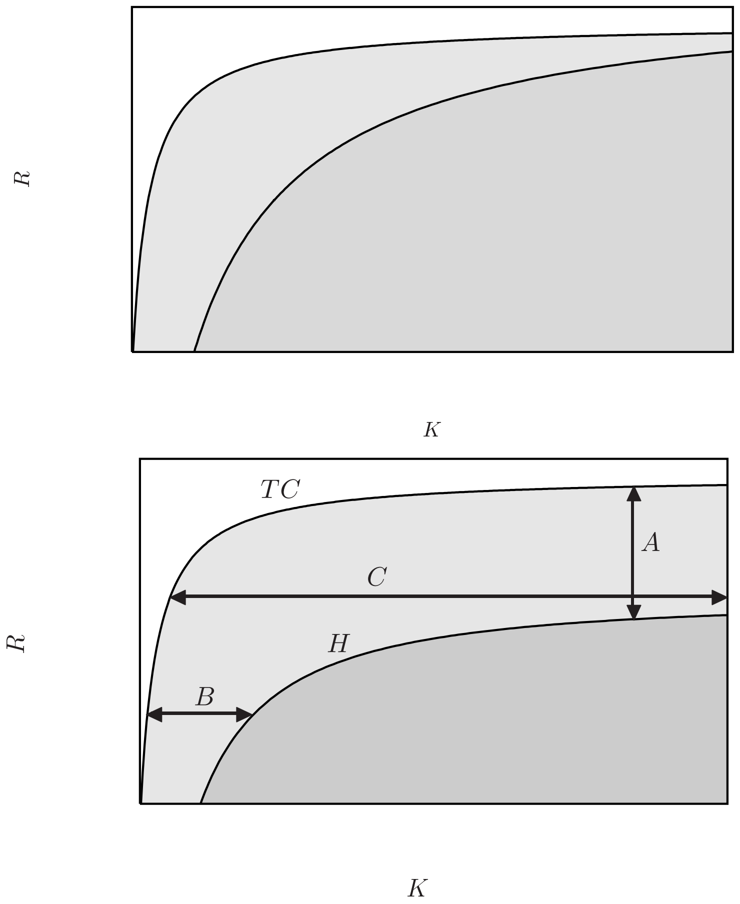

FIGURE 1. Demonstration of two types of stability in two-parameter bifurcation sketches. Upper panel: weak stability. The transcritical and Hopf bifurcations approach each other for $K \to \infty$. Lower panel: strong stability. The transcritical and Hopf bifurcation have different asymptotic values of R for $K \to \infty$. In the BD model for $T_I = 0$ holds that the distance $A = 0$, while for an increase in T_I the distance A also increases. There is a value $T_I = \tilde{T}_I$ where A is maximal.

4.2. **Results.** We proceed with discussing the bifurcation analysis of the generalized model. In the generalized analysis, we have two solutions of $det(\mathbf{J}) = 0$ for the positive equilibrium, namely $m = 1, \gamma_2 = 0$ and $\gamma_1/\gamma_2 = 1/n - 2$. Since $0 \leq n \leq 1$ and $\gamma_1/\gamma_2 < -1$, the latter condition cannot be satisfied in the BD model. However, in the following we will consider the case $\gamma_1/\gamma_2 = -1$ as the boundary of validity of the BD model. As we will see, the first condition is exactly the TC of the BD and RM models. The analysis of the zero equilibrium $\tilde{\mathbf{X}}$ yields the condition $\alpha_{21} = \alpha_{22}$ for the transcritical bifurcation. However, at the transcritical bifurcation where the positive equilibrium $\mathbf{X}^*$ intersects with the zero equilibrium $\tilde{\mathbf{X}}$ we have not only $\alpha_{21} = \alpha_{22} = \alpha_2$, but also $\mathbf{X}^* = \tilde{\mathbf{X}}$, and therefore $m = X_1^*/K = \tilde{X}_1/K = 1, n = \tilde{n}\tilde{X}_2 = 0$ and $\tilde{g}(x_1, x_2) = g(x_1, x_2)$. This shows

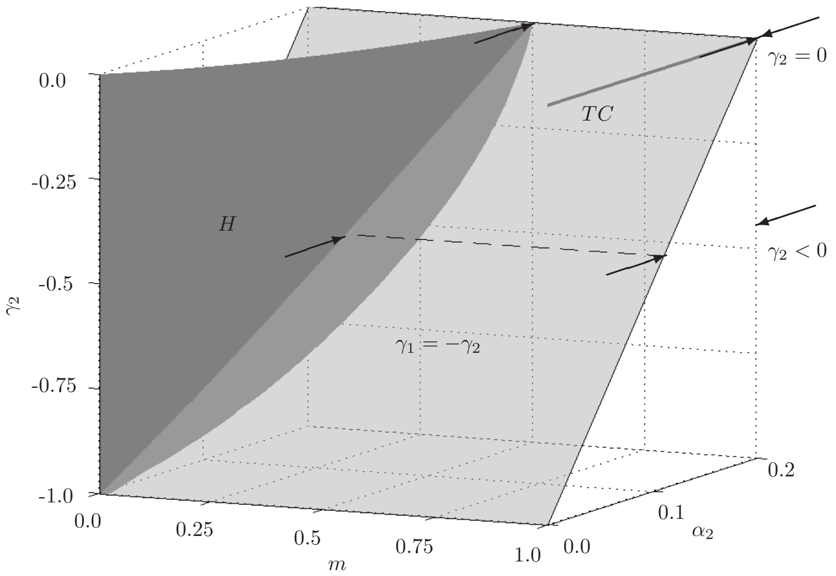

FIGURE 2. Three-dimensional local bifurcation diagram of the generalized model, with the BD functional response. The Hopf bifurcation surface is bounded by a curve where two eigenvalues are zero; *i.e.*, $det(\mathbf{J}) = 0$. However, this boundary is never reached, because the plane $\gamma_1 = -\gamma_2$, for which $K \to \infty$, prevents this.

that the condition for the positive equilibrium $m = 1, \gamma_2 = 0$ satisfies equally the condition for the zero equilibrium.

Figure (2) shows the bifurcation diagram of the generalized model if we assume $\gamma_1 = 1 - \alpha_2/\mu$ with $\mu = 0.2$. The transcritical bifurcation is the line $(m, \gamma_2) = (1, 0)$. The Hopf bifurcation surface is given by Equation (25) and limited by the conditions $det(\mathbf{J}) > 0$ (computed using an algorithm developed in [37]). For the BD model, only the parameter space above the surface $\gamma_2 = -\gamma_1 = 1 - \alpha_2/\mu$ is of interest, and for the RM model only the plane $\gamma_2 = 0$.

First, we observe that the Hopf bifurcation line in the plane $\gamma_2 = 0$ does not approach the TC at $m = 1$, but instead ends at $m = 0.5$ for $\alpha_2 = R = \mu = 0.2$. Second, for $K \to \infty$ we would expect $m \to 0$, so that the distance between the H and TC would increase with increasing K. In the RM model, however, we find that $X_1^* = T_S R/(\kappa - RT_H)$. By substitution of the parameters in the generalized Hopf condition Equation (25), and using the relations in equations (29, 30), where $\gamma_2 = 0$ for the RM model, we get the solution $m = X_1^*/K = R/(R + \mu)$. This results in

$$\frac{T_S R}{\kappa - RT_H} - \frac{KR}{R + \mu} = 0\ . \tag{32}$$

Since μ and κ are assumed to be constant this condition results in $R \to 0.2$ for $K \to \infty$, since $T_H = \kappa/\mu$. In return we find that $m = X_1^*/K = R/(R + \mu) \to 0.5$

for $K \to \infty$. Therefore, the Hopf bifurcation curve approaches indeed the point $(m = 0.5, \alpha_2 = \mu = 0.2, \gamma_2 = 0)$ for $K \to \infty$.

The above, however, does not explain our first observation. The distance between the TC and the Hopf bifurcation that becomes zero in the conventional bifurcation diagram for $K \to \infty$ is the distance in $R = \alpha_2$. But this distance becomes zero in the generalized bifurcation diagram as well. Both bifurcation lines H and TC in the generalized bifurcation diagram for the RM model ($\gamma_2 = 0$) end at the plane $\alpha_2 = R = \mu = 0.2$. This is the same limit value as in the conventional bifurcation analysis.

In the case of the BD model ($T_I > 0$) we have $\gamma_2 < 0$ for the Hopf bifurcation (considering the positive equilibrium $X_2^* > 0$) and $\gamma_2 = 0$ for the TC. The TC is the same as in the RM model with the limit value $\alpha_2 = R = \mu = 0.2$. Because of the restriction $\gamma_2 > -\gamma_1 = \alpha_2/\mu - 1$, we immediately see that for any $\gamma_2 < 0$ there is a finite distance between the Hopf bifurcation surface and the surface $\alpha_2 = 0.2$. Thus the Hopf bifurcation cannot reach the limit value of the TC anymore, leading to strong stabilization.

Let us now discuss how the conventional and generalized bifurcation diagrams are connected in detail. Figure 3 shows the results of continuations of bifurcations in K and R in the conventional model and how they display in the generalized model, where the default values for the vital parameters are adopted from Table 1 and $T_I = 1$. Curve (1) is a one-parameter continuation in K with $R = 0.08$, while curve (2) is a one-parameter continuation in R with K fixed. Both curves terminate on the transcritical bifurcation line TC and on the Hopf bifurcation surface H. Starting a two-parameter continuation in K and R on the Hopf bifurcation then results in the curve (3), for decreasing values of these parameters, and curve (4), for $K \to \infty$.

The same figure also shows the conditions for which *complete* stabilization occurs. From Equation (11) it can be derived that for $R \to 0$ the value of $\tilde{T}_I \to 1/r$. A one-parameter continuation in R for $K \to \infty$ from the TC to the Hopf bifurcation surface is always a straight line starting at $(m, \alpha_2, \gamma_2) = (1, 0.2, 0)$ and ending at the curve S, depending on the value of T_I. When $T_I = 2$, the end of the continuation line (the straight line labeled $T_I = 2$) coincides with the Hopf bifurcation surface in $(m, \alpha_2, \gamma_2) = (0, 0, -1)$ (recall that $r = 0.5$ and fixed). This means that in the case of $T_I > 2$ no destabilization *at all* occurs.

5. **Discussion.**

The stability of food chains has been discussed extensively in the theoretical ecological literature, and several model mechanisms have been proposed that work stabilizing. For instance, in [6] it was concluded that intraspecific predator interactions strongly stabilize the BD model dynamics. However, one note of criticism has been raised with regard to the ambiguous use of the term "stability" that makes it difficult to draw comparable conclusions [11, 31].

The stability classification given in this paper is based on local bifurcation analysis, and compares the limit cases of two biologically interpretable bifurcations under enrichment. The strong stabilization in the BD model corresponds to the existence of a region in parameter space where even infinite enrichment does not lead to limit cycles. There is also a minimal amount of intraspecific interactions $T_I = \tilde{T}_I$ for which this parameter region is maximal.

Other nonexclusively prey-dependent functional responses display the same type of stabilization, although the results are not shown here. We mention the presence

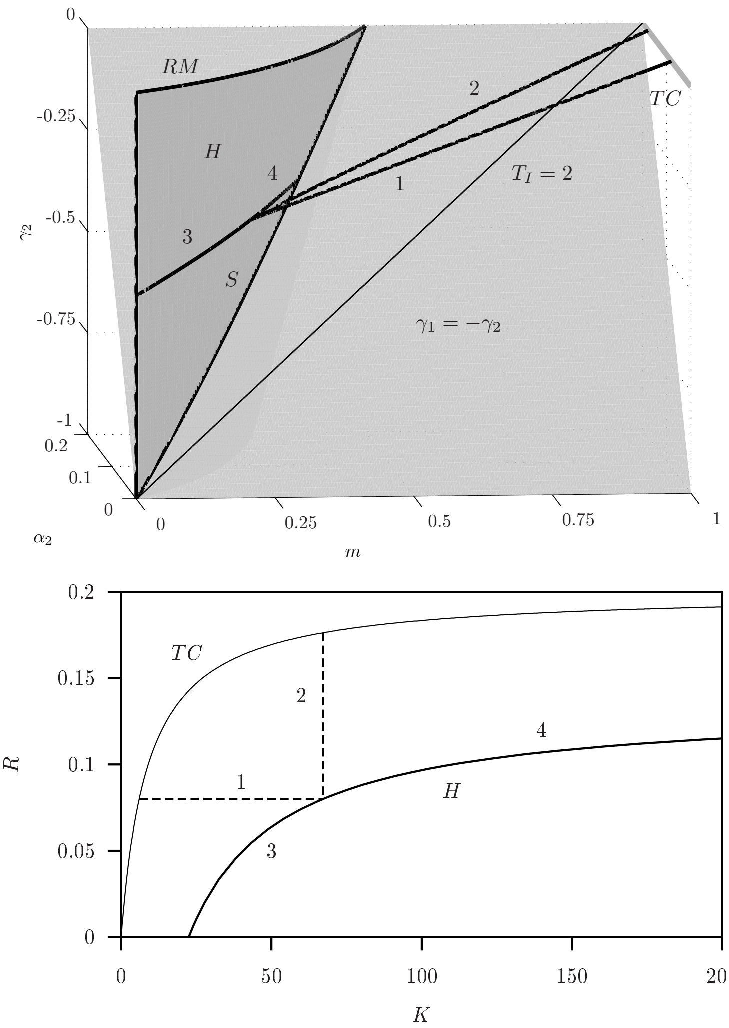

FIGURE 3. Continuation curves in one (K) and two (K and R) parameters, with $R = 0.08$ if fixed and $T_I = 1$. Upper panel: Three-parameter bifurcation diagram of the generalized BD model. Lower panel: Two-parameter bifurcation diagram in K and R of the conventional BD model. For explanation, see text. Observe that the curve S is the intersection curve of the Hopf bifurcation surface with the plane $\gamma_1 = -\gamma_2$.

of inedible prey species [25, 41], induced defenses in prey species [39], predator cannibalism [23], and the presence of hawk-dove tactics in the predator [2].

In an attempt to generalize these results we apply the normalization method by Gross et al. [14, 15, 13]). The used stability classification also works in the generalized formulations of the RM and BD models, but in a slightly different way than expected. There is no convergence of the Hopf bifurcation to the transcritical bifurcation corresponding to $m = 1$ in the generalized parameter space. The Hopf bifurcation surface in the generalized model is bounded by the equality $\gamma_1 = -\gamma_2$ for $K \to \infty$. For the RM model, this boundary coincides with the boundary of $\alpha_2 = \mu = 0.2$. In the BD model, this value of α_2 is not reached; instead, the continuation curves in K and R and thus the Hopf bifurcation curve are bounded by $\gamma_1 = -\gamma_2$ only. Although this effect is not intrinsic in the generalized model and cannot be understood without comparison to the conventional formulation of the model, we gain insight in the way how stabilization works.

Although the comparison between the conventional and generalized formulations of the RM and BD models results in better understanding of the stability properties of the two models, these results are not at all applicable in general. Other functional response functions than the ones discussed here may generate other dependencies of the scaling or generalized parameters, or both. The limitation caused by the equality $\gamma_1 = -\gamma_2$, that is vital for the strong stabilization, is specific for the used functional response(s) and might not exist in other models. Instead, other limitations may exist that alter the stability properties in turn.

Additionally, in many systems there exist more than one positive equilibrium for the same parameter set. In this case one has to do the analysis for each of the equilibria separately and then combine these analyses. It might happen that different equilibria are related to different stabilization effects. Note that for conventional models the bifurcation points for different equilibria can be combined in a single diagram. In generalized models the bifurcation diagram is independent of the specific equilibrium and therefore identical for all equilibria of the model.

The classification of stabilization is demonstrated only with models of two interacting species. Nevertheless, the whole method can be extended to models where more species interact. However, then one cannot use the trace of the Jacobian as the condition for the appearance of Hopf bifurcations, but one has to resort to a different method, for instance the method of resultants [12].

This paper shows that the combination of the generalized model approach and conventional approaches of the RM and BD models can lead to a better understanding of destabilization effects. The approach of generalized models was originally used to analyze systems where the functional forms of some processes are not known in detail. Points in the generalized parameter space represent a class of conventional models. Therefore it is difficult to identify where exactly in this generalized parameter space a given conventional model is located. Though the conclusions that can be drawn from the stability analysis of generalized models are much more general as demonstrated in [14], we restrict ourselves here to a generalized formulation of specific conventional models in order to compare the two methods and to show their equivalence. As it is demonstrated above, the bifurcation curves are bounded in parameter space if we specify the processes (*i.e.*, the functional response) in the generalized formulation. For this reason, not the whole generalized parameter space is represented in each conventional model of the same class. However, as we have shown these boundaries can explain the stability properties with respect to certain parameters of the conventional models, that we classify as either weakly or strongly stabilizing. As such, the generalized model formulation contributes to our understanding of the stability of equilibria in simple food chain models.

REFERENCES

[1] P. Abrams and C. J. Walters, *Invulnerable prey and the paradox of enrichment* Ecology **77** (1996), 1125–33.

[2] P. Auger, B. W. Kooi, R. B. Bravo de la Parra and J.-C. Poggiale, *Bifurcation analysis of a predator-prey model with predators using hawk and dove tactics*, J. Theor. Biol. **238** (2006), 597–607.

[3] A. D. Bazykin, "Nonlinear Dynamics of Interacting Populations," World Scientific, Singapore, 1998.

[4] J. R. Beddington, *Mutual interference between parasites or predators and its effect on searching efficiency*, J. Anim. Ecol. **44** (1975), 331–40.

[5] B. Boldin, *Introducing a population into a steady community: The critical case, the center manifold and the direction of the bifurcation*, SIAM J. Appl. Math. **66** (2006) 1424–53.

[6] D. L. DeAngelis, R. A. Goldstein and R. V. O'Neill, *A model for trophic interaction*, Ecology **56** (1975), 881–92.

[7] G. F. Fussman and B. Blasius., *Community response to enrichment is highly sensitive to model structure*, Biol. Lett. **1** (2005), 9–12.

[8] M. Genkai-Kato and N. Yamamura, *Unpalatable prey resolves the paradox of enrichment*, Proc. R. Soc. Lond. B. Biol. Sci. **266** (1999) 1215–19

[9] M. E. Gilpin, *Enriched predator-prey systems: Theoretical stability*, Science **177** (1972), 902–4.

[10] S. A. Gourley and Y. Kuang, *A stage structured predator-prey model and its dependence on maturation delay and death rate*, J. Math. Biol. **49** (2004), 188–200.

[11] V. Grimm and C. Wissel, *Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion*, Oecologia **109** (1997), 323–34.

[12] T. Gross and U. Feudel, *Analytical search for bifurcation surfaces in parameter space*, Physica D **195** (2004), 292–302.

[13] T. Gross and U. Feudel, *Generalized models as a universal approach to the analysis of nonlinear dynamical systems*, Phys. Rev. E. **73** (2006), 016205.

[14] T. Gross, W. Ebenhöh and U. Feudel, *Enrichment and foodchain stability: The impact of different forms of predator-prey interaction*, J. Theor. Biol. **227** (2004), 349–58.

[15] T. Gross, W. Ebenhöh and U. Feudel, *Long food chains are in general chaotic*, Oikos **109** (2005), 135–44.

[16] J. Guckenheimer and P. Holmes, "Nonlinear Oscillations, Dynamical Systems and Bifurcations of Vector Fields," Springer, Berlin, 1985, 2 Ed.

[17] A. Hastings, *Age-dependent predation is not a simple process. i. continuous time models*, Theor. Pop. Biol. **23** (1983), 347–62.

[18] A. Hastings, *Age-dependent dispersal is not a simple process: Density dependence, stability, and chaos*, Theor. Pop. Biol. **41** (1992), 388–400.

[19] C. S. Holling, *Some characteristics of simple types of predation and parasitism*, Can. Entomol. **91** (1959), 385–98.

[20] C. B. Huffaker, K. P. Shea and S. G. Herman, *Experimental studies on predation: Complex dispersion and levels of food in an acarine predator-prey interaction*, Hilgardia **34** (1963), 305–30.

[21] V. A. A. Jansen, *Regulation of predator-prey systems through spatial interactions: a possible solution to the paradox of enrichment*, Oikos **74** (1995), 384–90.

[22] K. L. Kirk, *Enrichment can stabilize population dynamics: Autotoxins and density dependence*, Ecology **79** (1998), 2456–62.

[23] C. Kohlmeier and W. Ebenhöh, *The stabilizing role of cannibalism in a predator-prey system*, Bull. Math. Biol. **57** (1995), 401–11.

[24] B. W. Kooi, *Numerical bifurcation analysis of ecosystems in a spatially homogeneous environment*, Acta Biotheor. **51** (2003), 189–222.

[25] M. Kretzschmar, R. M. Nisbet and E. McCauley, *A predator–prey model for zooplankton grazing on competing algal populations*, Theor. Popul. Biol. **44** (1993), 32–66.

[26] Y. A. Kuznetsov, "Elements of Applied Bifurcation Theory," Springer-Verlag, New York, 2004, 3rd Ed.

[27] I. Loladze, Y. Kuang and J. J. Elser, *Stoichiometry in producer-grazer systems: Linking energy flow with element cycling*, Bull. Math. Biol. **62** (2000), 1137–62

[28] H. Matsuda, P. A. Abrams and H. Hori, *The effect of adaptive antipredator behavior on exploitative competition and mutualism between predators*, Oikos **68** (1993), 549–59.

[29] S. Petrovskii, B.-L. Li and H. Malchow, *Transition to spatiotemporal chaos can resolve the paradox of enrichment*, Ecol. Complex. **1** (2004), 37–47.

[30] B. C. Rall, C. Guill and U. Brose, *Food-web connectance and predator interference dampen the paradox of enrichment*, Oikos **117** (2008), 202–13.

[31] S. Rinaldi and A. Gragnani, *Destabilizing factors in slow-fast systems*, Ecol. Modell. **180** (2004), 445–60.

[32] M. L. Rosenzweig, *Paradox of enrichment: Destabilization of exploitation ecosystems in ecological time*, Science **171** (1971), 385–87.

[33] M. L. Rosenzweig and R. H. MacArthur, *Graphical representation and stability conditions of predator-prey interactions*, Am. Nat. **97** (1963), 209–23.

[34] S. Roy and J. Chattopadhyay, *The stability of ecosystems: A brief overview of the paradox of enrichment*, J. Biosci. **32** (2007), 421–8.

[35] G. D. Ruxton, W. S. C. Gurney and A. M. De Roos, *Interference and generation cycles*, Theor. Pop. Biol. **42** (1992), 235–53.

[36] M. Scheffer and R. J. De Boer, *Implications of spatial heterogeneity for the paradox of enrichment*, Ecology **76** (1995), 2270–7.

[37] D. Stiefs, T. Gross, R. Steuer and U. Feudel, *Computation and visualization of bifurcation surfaces*, Int. J. Bif. Chaos **18**, 2008, to appear.

[38] E. H. Van Nes and M. Scheffer, *A strategy to improve the contribution of complex simulation models to ecological theory*, Ecol. Mod. **185** (2005), 153–64.

[39] M. Vos, B. W. Kooi, D. L. DeAngelis and W. M. Mooij, *Inducible defences and the paradox of enrichment*, Oikos **105** (2004), 471–80.

[40] S. Wiggins, "Introduction to Applied Nonlinear Dynamical Systems and Chaos," Springer, New York, 1990.

[41] M. H. F. Wilkinson, *Predation in the presence of decoys: An inhibitory factor on pathogen control by bacteriophages or bdellovibrios in dense and diverse ecosystems*, J. Theor. Biol. **208** (2001), 27–36.

Received on December 11, 2007. Accepted on March 28, 2008

E-mail address: `george.van.voorn@falw.vu.nl`