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On the dynamics of discrete food chains: Low- and high-frequency behavior and optimality of chaos

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Abstract. In this paper we derive and analyze a discrete version of Rosenzweig's (Am. Nat. 1973) food-chain model. We provide substantial analytical and numerical evidence for the general dynamical patterns of food chains predicted by De Feo and Rinaldi (Am. Nat. 1997) remaining largely unaffected by this discretization. Our theoretical analysis gives rise to a classification of the parameter space into various regions describing distinct governing dynamical behaviors. Predator abundance has a local optimum at the edge of chaos.

1. Introduction

Discussion of the dynamical properties of food chains is often traced back to Rosenzweig (1973), who presents a detailed study of the properties of the equilibria of a continuous food chain. Rosenzweig mainly discussed five equilibria, one corresponding to each of the origin, plants in the absence of other species, and plant-herbivore interaction, and two corresponding to interaction between all species. If two equilibria of the last kind exist then at least one of them is unstable. Hence, four equilibria are important, one corresponding to each possible length of the food chain. Furthermore, Rosenzweig noted that an invading carnivore either stabilizes or destabilizes plant-herbivore dynamics. Such stability properties have been related to food chain length (cf. May (1971), May (1974), Pimm and Lawton (1977) and Pimm (1982)).

Freedman and Waltman (1977) opened up the possibility of relating the stabilizing properties of an invading carnivore to its unsaturatedness: An unsaturated carnivore keeps at least one interior equilibrium - if one exists - locally stable. Stabilizing properties related to unsaturatedness in continuous systems are well known in the case of two-trophic-level interaction (cf. Kuang and Freedman (1988) and Section 2). The stabilizing scenarios induced by invading carnivores were further studied with respect to enrichment by Oksanen, Fretwell, Arruda, and Niemelä (1981).

The possibly destabilizing properties of saturated invading carnivores have recently been discussed by many authors, including: Boer, Kooi, and Kooijmann

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(1998); De Feo and Rinaldi (1997); Gragnani, De Feo, and Rinaldi (1998); Kuznetsov and Rinaldi (1996); McCann and Yodzis (1995); Rinaldi and De Feo (1999); and Kuznetsov, De Feo, and Rinaldi (2001). Gragnani et al. (1998) pointed out that the dynamic complexity of a tritrophic food chain first increases with respect to enrichment and then decreases until the carnivore becomes extinct. Barren environments cannot support a third trophic level at all, and if a system is supplied slightly above this level, stable coexistence is feasible. As the environmental carrying capacity increases stable coexistence does not become more possible, but rather low-frequency cyclic coexistence occurs. The dynamical complexity increases still further with enrichment, and chaotic coexistence follows. The tea-cup attractor (Hastings and Powell (1991)) found here describes a transition between low- and high-frequency cycles. If the carrying capacity is increased yet again, these attractors become cut tea-cup attractors and come to resemble increasingly simple cycles until a transition from chaos to cyclic behavior occurs. The cycles born of this transition have been called high-frequency cycles; they resemble two-dimensional herbivore-vegetation cycles in that the carnivore density remains almost constant during the oscillations. If the carrying capacity is increased at this level the mean carnivore density decreases, and if it is increased enough the carnivore goes extinct.

Depending on the exact choice of parameter values, one or several phases in the above scenario may be attenuated or absent. The stability of the herbivore-vegetation system can also be regulated independently of carnivore invasion. Thus, the boundary between the stabilizing and destabilizing scenarios is not sharp and certain mixes are allowed. Klebanoff and Hastings (1994) also give examples of how multiple attractors (initial value dependent behavior) may evolve.

In this paper we introduce a model for food-chain interaction with discrete birth processes. The suggested model is related in many ways to the models studied earlier by Gyllenberg, Hanski, and Lindström (1996), and Lindström (1999). In our model, vegetation can be a potential candidate for the lowest trophic level. Contest-type competition (Hassell (1974); Nicholson (1954)) is the typical competition type at this trophic level (cf. Łomnicki (1988)). The inclusion of such processes is not a straightforward process in our discrete setting. We must take into account dependencies arising from the fact that some individuals involved in the competition are removed by other processes, in our case grazing or predation. Dependencies limit how complicated we can make our models and remain one reason why continuous modeling has been preferred for modeling purposes (cf. Metz and Diekmann (1984)).

A procedure for including a dependence-generating, contest type of competition at the lowest trophic level in discrete models was suggested by Lindström (1999). In this paper we develop the approach taken in that paper, but because of the complexity of the model more restrictive assumptions are needed. In particular, we assume that all involved species display semelparity, meaning that they reproduce once within their lifetime (cf. Cole (1954)). Typical ecosystems possessing semelparity with non-overlapping generations at all trophic levels are those of terrestrial arthropods, see Borror, DeLong, and Triplehorn (1976). We further simplify by approximating by elementary functions all expressions involving exponential integrals. These estimates are chosen with care and are valid for large parts of the phase- and parameter-space.

We continue with a detailed analytical description of the introduced model. By means of the above simplifications we construct a special case that: (1) allows explicit formulation of the stability criteria and a complete bifurcation analysis at all fixed points; (2) allows high-quality numerical analysis; (3) guarantees boundedness of solutions; and (4) contains the basic general dynamical patterns of continuous food chains. Hence, we believe that the analysis presented below represents a procedure for analyzing more complicated discrete food chains.

2. Discrete versus continuous models for food chains

Several boreal organisms exhibit pulse-wise reproduction strategies driven by seasonality. One might ask what kinds of models would be suitable for describing such populations. Potential models should represent various mechanisms, such as growth and predator-prey interaction. Such populations have frequently been modeled using continuous models. These phenomenological modeling attempts have produced new angles of incidence (cf. Hanski, Hansson, and Henttonen (1991) and Oksanen et al. (1981)), and one may ask whether certain dynamical properties might be conserved when changing how interaction between different organisms is modeled. Our objective is not the formulation of a rough homomorphism that could specify the classification of different dynamical systems relevant to this setting; instead, we wish to make readers aware of what requirements such a theoretical formulation should meet.

It is not generally obvious how discrete and continuous models are related to each other. Several authors derive discrete population models simply by replacing differentials with differences. Such a discretization does not generally preserve any of the dynamical properties of the continuous model under consideration. The best-known example is the discrete logistic equation and the corresponding continuous one (May (1973)), in which not only radical differences in the dynamical properties can be observed. Population models should generally preserve the positive number of individuals, and this property is not conserved in the above case for all parameter values that could be biologically meaningful.

The approach we suggest starts with splitting the involved processes into birth and death processes. We want our approach to conform maximally with the seasonally driven, pulse-wise reproduction behavior observed in boreal populations. Therefore, we shall assume that only birth processes take place in discrete time while death processes remain continuous. For instance, the right-hand side of the continuous logistic model

$$\dot{x} = rx - cx - kx^2 \quad (1)$$

contains one term representing births, one term representing natural death, and one term representing death due to competition. We derive a discrete analogue of this model by integrating the death terms over the season. We assume that there were x_0 individuals present at the beginning of the season and that the season-length is T . Now define

$$\kappa(\gamma) = \begin{cases} \frac{1 - \exp(-\gamma)}{\gamma}, & \gamma > 0, \\ 1, & \gamma = 0. \end{cases} \quad (2)$$

The number of individuals that can reproduce at the end of the season is represented by

$$x(T) = \frac{x_0 \exp(-cT)}{1 + kTx_0\kappa(cT)}.$$

These individuals are assumed to multiply at a fixed birth rate, β . Our discrete logistic model takes the form proposed by Beverton and Holt (1957):

$$X_{t+1} = \frac{M_0 X_t}{1 + X_t} \tag{3}$$

after introducing $X = kTx_0\kappa(cT)$ and $M_0 = \beta \exp(-cT)$. We stress that the dynamics of the models (1) and (3) are very similar. If $M_0 > 1$, $k > 0$, and $r - c > 0$, then both models possess two nonnegative fixed points and their positive fixed points attract all positive initial values.

When two populations are involved, dynamical similarities do not more carry over that directly. In order to avoid certain complications and problems associated with modeling different age classes in the rest of the paper, we shall assume semelparity and neglect natural death for all species described by our discrete models. That is, the organisms reproduce once during their lifetimes and are removed from the population after reproducing.

The corresponding discretization of the Lotka (1925) and Volterra (1926) model is given by a model quite similar to the Nicholson and Bailey (1935) model:

$$\begin{aligned} X_{t+1} &= M_0 X_t \exp(-U_t), \\ U_{t+1} &= M_1 X_t (1 - \exp(-U_t)) \end{aligned}$$

(cf. Lindström (1999)) which is known to possess unbounded oscillations, see May (1973). We stress that the discrepancies between these two models provide no reason to stop exploring possible similarities between discrete and continuous models in this setting. The Lotka-Volterra model is structurally unstable, and even the continuous model closest to it could possess the same dynamical discrepancies.

The Gause (1934) predator-prey model

$$\begin{aligned} \dot{x} &= rx - c_1x - kx^2 - \frac{ax}{1 + ahx}y, \\ \dot{y} &= m \frac{ax}{1 + ahx}y - c_2y \end{aligned}$$

is a better candidate to start with when comparing the dynamical properties of continuous and discrete models. In both equations, the first two terms describe the growth and natural deaths of the involved prey, x , and its predator, y . The third term describes intraspecific competition, and the fourth, predation, according to the Holling II functional response, see Holling (1959). The model includes two parameters not included in the original Lotka-Volterra system. The first is the intraspecific competition coefficient, $k > 0$, and the second is the time needed for handling the prey, $h > 0$. The basic dynamical properties of the Gause model can be described as follows: Let the carrying capacity, $(r - c_1)/k$, be the bifurcation

parameter of the system and assume that $m > hc_2$. If the carrying capacity is kept below $c_2/a(m - hc_2)$, then the predator becomes extinct. Stable coexistence occurs when

$$\frac{c_2}{a(m - hc_2)} < \frac{r - c_1}{k} \leq \frac{2c_2}{a(m - hc_2)} + \frac{1}{ah} \quad (4)$$

and oscillatory coexistence occurs for still higher carrying capacities, (cf. Kuang and Freedman (1988)).

If no handling time ($h = 0$) were assumed, the stage with oscillatory coexistence would be omitted, since the last term in (4) becomes infinite. There are several reasons for including the handling time in ecological models, but in this context we focus on the need to include it in order to produce a predator-prey model with a full range of dynamical behavior. In contrast, it turns out that several discrete versions of the Gause predator-prey model derived by integrating various death terms over the season length and taking into account the dependencies arising between them already produce the full range of dynamical behavior with respect to the carrying capacity, without assigning a handling time greater than zero. For instance, the model

$$\begin{aligned} X_{t+1} &= \frac{M_0 X_t \exp(-U_t)}{1 + X_t \kappa(U_t)}, \\ U_{t+1} &= M_1 X_t (1 - \exp(-U_t)). \end{aligned} \quad (5)$$

will be a relevant submodel of the food chain studied later on. As in the continuous case above, members of the lowest trophic level are assumed to compete directly for some resources, setting an upper limit to their density. We name that quantity the environmental carrying capacity. It turns out that it is represented by $M_0 - 1$ in (5). Model (5) predicts extinction of the second trophic level, U , at low carrying capacities, possibilities for stable coexistence at moderate carrying capacities, and oscillatory coexistence at high carrying capacities. Similar results for related discrete models can be found in Lindström (1999).

A main thrust of this paper is to explore whether such similarities can be found between discrete and continuous food chains. That is, when the dynamics for a discrete and a continuous food chain are followed at increasing carrying capacities, is it plausible to expect similar dynamical patterns? And what kind of attention should be made when defining the word “similar” here? Since food chains are discussed in the sequel, we refer to the first trophic level of these models as “vegetation”, the second as “herbivores”, and the third as “carnivores” in the rest of the paper. According to this terminology, the predator-prey model (5) will be referred to as a vegetation-herbivore model, and the single-species model (3) will be referred to as the corresponding vegetation model.

3. A discrete model for a food chain

In this section we build up our main model. We assume that both carnivores and herbivores are unsaturated, and divide the vegetation into plants receiving sufficient light for reproduction at the beginning of the next season and plants not doing

so. At the beginning of the season all emerging plants have the potential to reproduce, but as the season goes on more of them are excluded. For simplicity, we assume that this exclusion process is governed by the third term of (1). We also assume that vegetation excluded from reproduction remains in the population and remains just as exposed to herbivores as vegetation having the potential to reproduce. We obtain the following equations for the death processes (cf. Lindström (1999)):

$$\begin{aligned} \dot{x}_R &= -kx_R^2 - ax_Ry, & x_R(0) &= x_0, \\ \dot{x}_F &= +kx_R^2 - ax_Fy, & x_F(0) &= 0, \\ \dot{y} &= -byz, & y(0) &= y_0, \\ \dot{z} &= 0, & z(0) &= z_0. \end{aligned}$$

Here x_R denotes reproducing plants, x_F represents plants excluded from reproduction, and y and z denote herbivore and carnivore abundance, respectively. The parameter, k , describes competition among plants, while a and b describe the search rates for herbivores and carnivores, respectively. We have assumed no natural death, semelparity being one justification for this, since all individuals will live just one season. Define $x = x_R + x_F$ so that $\dot{x} = -axy$. We solve the above system of equations and obtain:

$$\begin{aligned} x(t) &= x_0 \exp\left(-ay_0t \cdot \frac{1 - \exp(-bz_0t)}{bz_0t}\right), \\ y(t) &= y_0 \exp(-bz_0t), \\ z(t) &= z_0. \end{aligned}$$

These equations denote the individuals still alive at the end of the season. In the case of plants, some of them are able to reproduce. These are denoted by:

$$x_R(t) = \frac{x_0 \exp\left(-ay_0t \cdot \frac{1 - \exp(-bz_0t)}{bz_0t}\right)}{1 + \frac{kx_0t}{bz_0t} \exp\left(-\frac{ay_0t}{bz_0t}\right) \left(\text{Ei}\left(\frac{ay_0t}{bz_0t}\right) - \text{Ei}\left(\frac{ay_0t}{bz_0t} \exp(-bz_0t)\right)\right)},$$

where

$$\text{Ei}(x) = \int_{-\infty}^x \frac{\exp(\xi)}{\xi} d\xi.$$

is to be evaluated as a Cauchy principal value.

Next, assume that the reproducing plants, x_R , produce a mean of M_0 offspring at the time instant, T . Simultaneously, we assume that a fraction of the consumed vegetation and herbivore biomass is converted into herbivore and carnivore biomass, respectively. We take into account the fact that the entirety of this consumption does not correspond to the biomass of herbivores or carnivores alive at the end of the season. We get

$$\begin{aligned}
 x(T) &= \frac{M_0 x_0 \exp\left(-a y_0 T \cdot \frac{1 - \exp(-b z_0 T)}{b z_0 T}\right)}{1 + \frac{k x_0 T}{b z_0 T} \exp\left(-\frac{a y_0 T}{b z_0 T}\right) \left(\text{Ei}\left(\frac{a y_0 T}{b z_0 T}\right) - \text{Ei}\left(\frac{a y_0 T}{b z_0 T} \exp(-b z_0 T)\right)\right)}, \\
 y(T) &= m_1 x_0 a y_0 T \cdot \exp(-b z_0 T) \cdot \frac{1 - \exp\left(-a y_0 T \cdot \frac{1 - \exp(-b z_0 T)}{b z_0 T}\right)}{a y_0 T}, \\
 z(T) &= m_2 y_0 b z_0 T \cdot \frac{1 - \exp(-b z_0 T)}{b z_0 T},
 \end{aligned}$$

if we assume semelparity at all trophic levels. Now introduce

$$\begin{aligned}
 X &= k x_0 T, \\
 Z &= b z_0 T, \\
 M_1 &= m_1 a / k, \\
 M_2 &= m_2 b / a, \\
 H(\alpha, \rho) &= -\exp(-\rho)(\text{Ei}(\rho) - \text{Ei}(\alpha\rho)) / \log \alpha, \\
 U &= a y_0 T \kappa(b z_0 T).
 \end{aligned}$$

Observe that κ was defined by (2). We can assume $T = 1$ without loss of generality and obtain

$$\begin{aligned}
 X_{t+1} &= \frac{M_0 X_t \exp(-U_t)}{1 + X_t H\left(\exp(-Z_t), \frac{U_t}{1 - \exp(-Z_t)}\right)}, \\
 U_{t+1} &= M_1 X_t U_t \exp(-Z_t) \kappa(U_t) \cdot \kappa(M_2 U_t Z_t), \\
 Z_{t+1} &= M_2 U_t Z_t.
 \end{aligned} \tag{6}$$

It follows from Lindström (1999), Proposition 3.1(f), that the rather complicated function, H , can be estimated by

$$H(\exp(-Z), U/(1 - \exp(-Z))) \approx \max(\exp(-U), \kappa(Z)\kappa(U)).$$

and that the system to be studied takes the form

$$\begin{aligned}
 X_{t+1} &= \frac{M_0 X_t \exp(-U_t)}{1 + X_t \max(\exp(-U_t), \kappa(Z_t)\kappa(U_t))} \\
 U_{t+1} &= M_1 X_t U_t \exp(-Z_t) \kappa(U_t) \cdot \kappa(M_2 U_t Z_t) \\
 Z_{t+1} &= M_2 U_t Z_t.
 \end{aligned} \tag{7}$$

We replaced the model (6) with (7) throughout the rest of the paper and we think some remarks justifying this choice are necessary here. First, local stability analysis can be made theoretically for large areas of the parameter space for (7). Second, we have so far been unable to produce a numerical representation of

$$\begin{aligned}
 \frac{\partial H\left(e^{-Z}, \frac{U}{1 - \exp(-Z)}\right)}{\partial Z} &= \frac{\exp(-Z) - \exp(-U)}{Z(1 - \exp(-Z))} + H\left(e^{-Z}, \frac{U}{1 - \exp(-Z)}\right) \\
 &\quad \times \left(-\frac{1}{Z} + \frac{U \exp(-Z)}{(1 - \exp(-Z))^2}\right)
 \end{aligned} \tag{8}$$

that could meet our criteria for numerical reliability at $Z < 10^{-4}$. We were thus unable to ensure the quality of our numerical results for (6) everywhere, and we have not explored whether all numerical representation problems connected to (6) are eliminated by solving these problems. Third, for parts of the parameter and phase space simultaneously corresponding to numerically reliable expressions for the right-hand side of (6) and its partial derivatives, only minor differences between the systems (6) and (7) were detected. See in particular remark (b) after Theorem 4.4.

Note that the vegetation-herbivore model (5) and the vegetation model (3) are submodels of (7) in the following way. We obtain (5) by substituting $M_2 = 0$ or $Z_t = 0$ into (7), and we obtain (3) by substituting $M_2 = M_1 = 0$ or $Z_t = U_t = 0$ into (7). Similarly, (3) is a submodel of (5).

We begin with the following basic lemma.

Lemma 3.1. *Solutions of (7) remain positive and bounded.*

Proof. Positiveness follows directly from the equations. From the equation for X_{t+1} , it follows that succeeding values of X_t are bounded by M_0 . From the equation for U_{t+1} we obtain

$$U_{t+2} < \frac{U_{t+2}}{\kappa(Z_{t+2})} < M_1 M_0.$$

From the last equation we obtain

$$Z_{t+3} < M_2 \frac{U_{t+2}}{\kappa(Z_{t+2})} Z_{t+2} \kappa(Z_{t+2}) < M_2 M_1 M_0,$$

in the next iteration. Thus, all solutions starting in the positive cone enter the box $0 < X < M_0, 0 < U < M_0 M_1, 0 < Z < M_0 M_1 M_2$ within three iterations. \square

The system (7) admits at most four equilibria, one corresponding to each possible length of the food chain. We label them as $(0, 0, 0), (M_0 - 1, 0, 0), (X_*, U_*, 0)$, and $(\hat{X}, \hat{U}, \hat{Z})$. Circumstances that could produce an additional unstable equilibrium as in the continuous case (cf. Section 1), are thus not present in our discrete setting. The uniqueness $(\hat{X}, \hat{U}, \hat{Z})$ follows from the fact that the right-hand side of

$$1 = M_1 \frac{M_0 \exp(-1/M_2) - 1}{\max(\exp(-1/M_2), \kappa(1/M_2)\kappa(Z))} \kappa(1/M_2) \exp(-Z) \kappa(Z)$$

is a continuous and strictly decreasing function of Z . Since the XZ plane and the UZ plane do not introduce any new asymptotic behavior, the persistence criteria for vegetation and herbivores remain unchanged with respect to the herbivore-vegetation system. That is, if $M_0 > 1$ and $M_0 > (M_1 + 1)/M_1$, then vegetation and herbivores respectively persist.

The following lemma shows, together with the dynamical properties of the herbivore-vegetation system, that the persistence criteria for carnivores must be considered separately and can be difficult to formulate. The proof of the lemma follows from the equation for Z_{t+1} in (7).

Lemma 3.2. *If*

$$\lim_{n \rightarrow \infty} \sqrt[n]{\prod_{i=0}^{n-1} U_i} < \frac{1}{M_2}. \tag{9}$$

then (7) predicts $\lim_{n \rightarrow \infty} Z_n = 0$.

Lemma 3.2, together with Lemma 3.1, states that the asymptotic geometric mean of the herbivore population must equal $1/M_2$, otherwise the carnivores become extinct. Since asymptotic behavior of the herbivore-vegetation system normally includes multiple attractors (cf. Aronson, Chory, Hall, and McGehee (1982)) it can be a delicate matter to determine whether all possible coexisting attractors have the same properties with respect to (9). As long as this question remains unanswered there might be one attractor in the herbivore-vegetation plane that would allow local carnivore invasion, together with one giving rise to local extinction. However, according to our numerical analysis it seems that what we are likely to observe is an interval with respect to M_0 which allows carnivore invasion and persistence. This can be explained in two ways: either possible coexisting attractors possess asymptotic geometric means which remain close to each other, or carnivore invasion usually occurs for parameter values that do not allow multiple attractors in the herbivore-vegetation system.

4. Equilibria

As concluded in Section 3, (7) possesses at most four equilibria which we referred to as $(0, 0, 0)$, $(M_0 - 1, 0, 0)$, $(X_\star, U_\star, 0)$, and $(\hat{X}, \hat{U}, \hat{Z})$. The Jacobian of (7) evaluated at the first two of these equilibria allows triangular or diagonal representation, and thus the stability properties of these equilibria are simple. The coordinates of the third equilibrium are given by

$$(X_\star, U_\star, 0) = \left(\frac{M_0 \log \left(\frac{M_1 M_0}{1 + M_1} \right)}{(M_0 - 1)M_1 - 1}, \log \left(\frac{M_1 M_0}{1 + M_1} \right), 0 \right). \tag{10}$$

The second coordinate of (10) and Lemma 3.2 give:

Corollary 4.1. *The carnivore abundance decreases near $(X_\star, U_\star, 0)$, if*

$$M_0 < \exp(1/M_2)(M_1 + 1)/M_1. \tag{11}$$

The carnivore abundance increases near $(X_\star, U_\star, 0)$, if the converse inequality holds.

On the basis of the above corollary we know all the stability properties of (10) which are related to motion outside the invariant XU plane. We shall therefore restrict further stability analysis of (10) to that plane. The system, (7), restricted accordingly takes the form (5). The next theorem follows using the ideas of Lindström (1999); its proof is included for convenience.

Theorem 4.2. *The equilibrium (10) is locally stable in the invariant XU plane when*

$$\frac{M_0 \log \frac{M_1 M_0}{1+M_1}}{(M_0 - 1)M_1 - 1} < \frac{1}{M_1} \cdot \frac{M_1 + 2}{M_1 + 1} \tag{12}$$

and unstable when the converse inequality holds. If equality holds in (12), and M_0 is used as bifurcation parameter, then (10) undergoes a Hopf bifurcation.

Proof. Note that $\kappa'(U) = (\exp(-U) - \kappa(U))/U$. The Jacobian of the system (5) at (X_*, U_*) is given by

$$J_*(X_*, U_*) = \begin{pmatrix} \frac{M_1}{M_1+1} & -\frac{X_*}{U_*} \frac{M_1 U_* + M_1 X_* - 1}{M_1 X_* - U_*} \\ U_*/X_* & M_1 X_* - U_* \end{pmatrix} \tag{13}$$

We require

$$-1 + |\text{Tr} J_*(X_*, U_*)| - \det J_*(X_*, U_*) < 0, \tag{14}$$

$$-1 + \det J_*(X_*, U_*) < 0 \tag{15}$$

for local stability and obtain

$$\begin{aligned} \text{Tr} J_*(X_*, U_*) &= \frac{M_1}{M_1 + 1} + M_1 X_* - U_* \\ \det J_*(X_*, U_*) &= \frac{M_1^2 X_* + M_1 X_* - 1}{M_1 + 1} \end{aligned}$$

Since $U_* < M_1 X_*$, expression (14) is equivalent to $-U_* < 0$, which is identically true. It follows from the relationship between roots and coefficients of a quadratic equation that if (X_*, U_*) undergoes a bifurcation, then $J_*(X_*, U_*)$ must possess complex eigenvalues with positive real parts. Thus, strong resonances connected to a discrete Hopf bifurcation are excluded.

We proceed to (15). It states that (X_*, U_*) is stable if

$$X_* < \frac{1}{M_1} \cdot \frac{M_1 + 2}{M_1 + 1}, \tag{16}$$

and unstable if the converse inequality holds. Since X_* is a strictly increasing function of M_0 , the transversality condition holds using M_0 as bifurcation parameter. It follows that the Hopf bifurcation occurs for exactly one value of M_0 as it increases. Strong resonances were earlier excluded and substitution of (10) in (16) gives the stability criterion (12). □

We proceed with the fourth equilibrium $(\hat{X}, \hat{U}, \hat{Z})$. As long as

$$\max(\exp(-\hat{U}), \kappa(\hat{U})\kappa(\hat{Z})) = \kappa(\hat{U})\kappa(\hat{Z}) \tag{17}$$

it is given by

$$\left(\frac{M_0 e^{-1/M_2} - 1}{\kappa\left(\frac{1}{M_2}\right) \kappa\left(\log M_1\left(M_0 e^{-\frac{1}{M_2}} - 1\right)\right)}, \frac{1}{M_2}, \log M_1\left(M_0 e^{-\frac{1}{M_2}} - 1\right) \right). \tag{18}$$

We point out that there are parameter values M_0 , M_1 , and M_2 , such that (18) yields the relevant coordinates for $(\hat{X}, \hat{U}, \hat{Z})$, as long as it remains locally stable. We have mainly focused on those parameter values in our numerical study (Section 5), but we also considered other parameter values (Figure 4(c)-(d)). The following lemma gives some preliminary estimates needed for the proof of the next theorem. The lemma follows from the equation for U_{t+1} in (7) and (2).

Lemma 4.3. *We have:*

- (a) $\max(1, \hat{U}) < \frac{1}{\kappa(\hat{U})} = M_1 \hat{X} \exp(-\hat{Z}) \kappa(\hat{Z})$,
- (b) $0 < -\frac{\kappa'(\hat{Z})}{\kappa(\hat{Z})} = \frac{\kappa(\hat{Z}) - \exp(-\hat{Z})}{1 - \exp(-\hat{Z})} < \kappa(\hat{Z})$.

Theorem 4.4. *Let $\mathcal{M} = M_1 \exp(-\hat{Z})$ and $\mathcal{K} = -\kappa'(\hat{Z})/\kappa(\hat{Z})$. Assume (17) and*

$$M_1 > \min\left(1 - \exp\left(-\frac{1}{M_2}\right), \kappa\left(\frac{1}{M_2}\right)\right). \tag{19}$$

The equilibrium (18) is locally stable if

$$\mathcal{M} \hat{X} \kappa(\hat{Z}) < \frac{2 + \mathcal{M} - \mathcal{M} \hat{Z} - \mathcal{K} \hat{Z}}{1 + \mathcal{M}} - \frac{\hat{Z}}{\hat{U}(1 + \mathcal{M}) + \mathcal{K} \hat{Z}(2 + \mathcal{M}) + \mathcal{M} \hat{Z}} \tag{20}$$

and unstable when the converse inequality holds. If equality in (20) holds and M_0 is used as bifurcation parameter, then (18) undergoes a Hopf bifurcation.

Remarks

- (a) It will turn out that the real parts of the complex characteristic roots at the regular Hopf bifurcation are positive, so we expect periods larger than four to be observed. This is a first indication that herbivore-vegetation cycles cannot be distinguished from carnivore cycles by measuring periods close to a bifurcation, see Theorem 4.2 and its proof. Section 5 provides further evidence of this fact.
- (b) For some parameter values satisfying (17), (19), and (20), we also detected quasi- or high-periodic behavior, i.e. attractors involving alternatives to stable dynamics. One example is $M_0 = 3.052$, $M_1 = .9355$, and $M_2 = 4.0$. We did not observe multiple attractors for the smooth system (6) at the corresponding parameter values, so this phenomenon might have been introduced by our approximation (7). The parameter range possessing this phenomenon was usually narrow and hard to detect.
- (c) Condition (19) was needed in our proof to exclude strong resonances. It can probably be removed from the theorem but we did not find that this condition was too restrictive either.

(d) We conjecture that the implication (20) \Rightarrow (12) holds, but it seems difficult to construct a proof of this fact for the whole parameter range (17) and (19). Numerical experiments indicated that something similar also held outside (17) and (19). Remarkable ecological consequences follow if this implication remains true. May (1971) gave examples showing that food-web complexity does not generally increase stability. Our results show that our system constitutes no exception to this rule.

Proof. The Jacobian of (7) evaluated at (18) assumed (17) is represented by

$$\begin{pmatrix} \frac{\mathcal{M}}{\mathcal{M}+1} & -\frac{\hat{X}}{\hat{U}} \cdot \frac{\mathcal{M}\hat{U}+\mathcal{M}\hat{X}\kappa(\hat{Z})-1}{\mathcal{M}+1} & \frac{\hat{X}\mathcal{K}}{\mathcal{M}+1} \\ \hat{U}/\hat{X} & \mathcal{M}\hat{X}\kappa(\hat{Z}) - \hat{U} - \mathcal{K}\hat{Z} & -\hat{U} - \hat{U}\mathcal{K} \\ 0 & \hat{Z}/\hat{U} & 1 \end{pmatrix} \tag{21}$$

The characteristic equation of (21) takes the form

$$\begin{aligned} &\lambda^3 + \lambda^2 \frac{-1 + \hat{U} - \kappa(\hat{Z})\mathcal{M}^2\hat{X} + \mathcal{K}\hat{Z} - 2\mathcal{M} + \hat{U}\mathcal{M} - \kappa(\hat{Z})\mathcal{M}\hat{X} + \mathcal{M}\mathcal{K}\hat{Z}}{1 + \mathcal{M}} \\ &+ \lambda \frac{-1 - \hat{U} + 2\kappa(\hat{Z})\mathcal{M}^2\hat{X} + \hat{Z} + \mathcal{M} - \mathcal{M}\hat{U} + 2\kappa(\hat{Z})\mathcal{M}\hat{X} + \mathcal{M}\hat{Z} - \mathcal{M}\mathcal{K}\hat{Z}}{1 + \mathcal{M}} \\ &+ \frac{1 - \kappa(\hat{Z})\mathcal{M}\hat{X} - \kappa(\hat{Z})\mathcal{M}^2\hat{X} - \mathcal{K}\hat{Z} - \mathcal{M}\hat{Z}}{1 + \mathcal{M}} = 0 \end{aligned}$$

The Schur-Cohn criteria (see, for example, Schur (1917, 1918), Cohn (1922), Jury (1964), Marden (1966), and May (1974)) for the cubic equation

$$\lambda^3 + \alpha\lambda^2 + \beta\lambda + \gamma = 0$$

are given by

$$1 - \gamma^2 > |\alpha\gamma - \beta| \tag{22}$$

$$|1 + \beta| > |\alpha + \gamma| \tag{23}$$

Note that Lemma 4.3 yields

$$\gamma < 0, \tag{24}$$

$$\alpha < 0. \tag{25}$$

Condition (23) can be stated as

$$\begin{aligned} &|2\kappa(\hat{Z})\mathcal{M}^2\hat{X} - \mathcal{M}\hat{U} + 2\kappa(\hat{Z})\mathcal{M}\hat{X} - \hat{U} + \mathcal{M}\hat{Z} + 2\mathcal{M} - \mathcal{K}\mathcal{M}\hat{Z} + \hat{Z}| \\ &> |-2\kappa(\hat{Z})\mathcal{M}^2\hat{X} + \mathcal{M}\hat{U} - 2\kappa(\hat{Z})\mathcal{M}\hat{X} + \hat{U} - \mathcal{M}\hat{Z} - 2\mathcal{M} + \mathcal{K}\mathcal{M}\hat{Z}|. \end{aligned} \tag{26}$$

From Lemma 4.3 we obtain

$$\begin{aligned} &2\kappa(\hat{Z})\mathcal{M}^2\hat{X} - \mathcal{M}\hat{U} + 2\kappa(\hat{Z})\mathcal{M}\hat{X} - \hat{U} + \mathcal{M}\hat{Z} + 2\mathcal{M} - \mathcal{K}\mathcal{M}\hat{Z} \\ &= (\mathcal{M} + 1) \left(2\kappa(\hat{Z})\mathcal{M}\hat{X} - \hat{U} \right) + 2\mathcal{M} + (1 - \mathcal{K})\mathcal{M}\hat{Z} \\ &> (\mathcal{M} + 1) \left(2\kappa(\hat{Z})\mathcal{M}\hat{X} - \hat{U} \right) + 2\mathcal{M} + \left(1 - \kappa(\hat{Z}) \right) \mathcal{M}\hat{Z} > 0. \end{aligned} \tag{27}$$

Using (27) and $\hat{Z} > 0$ we can evaluate the absolutes in (26) and use $\hat{Z} > 0$ to conclude that (23) holds identically. It follows from the relationship between roots and coefficients of a cubic equation that a pair of complex eigenvalues must be involved in any exchange of stability of the fixed point (18).

Now consider (22). By (24), we require $-1 < \gamma < 0$ for stability. Depending on the sign inside the absolute sign, (22) assumes one of the following forms:

$$1 + \beta > \gamma(\gamma + \alpha), \tag{28}$$

$$1 - \beta > \gamma(\gamma - \alpha). \tag{29}$$

Superfluosness of (28) follows from (23), (24), and (27). Accordingly, possible bifurcations satisfy

$$1 - \beta = \gamma(\gamma - \alpha). \tag{30}$$

Let $\gamma_i, i = 1, 2$ be the two solutions of (30). Lemma 4.3 gives

$$-2 - \hat{U} + 2\kappa(\hat{Z})\mathcal{M}^2\hat{X} + \hat{Z} - \mathcal{M}\hat{U} + 2\kappa(Z)\mathcal{M}\hat{X} + \mathcal{M}(1 - \mathcal{K})\hat{Z} > \tag{31}$$

$$-\min(1, \hat{U}) + \frac{\mathcal{M}}{\kappa(\hat{U})} + \hat{Z} + \mathcal{M}(1 - \mathcal{K})\hat{Z} \tag{32}$$

which implies $\beta > 1$ for $M_1 \geq 1$ or $\hat{Z} \geq 1$. If $M_1 < 1$ and $\hat{Z} < 1$, then (32) increases with \hat{Z} and $\beta > 1$ follows from (19). It follows from (25) and (30) that $\alpha\beta < \alpha < \gamma_1 \leq \gamma_2 < 0$. Thus, the characteristic equation of (21) possesses the Hurwitz determinant sequence $\{1, \alpha, \alpha(\alpha\beta - \gamma), \gamma\}$, see Marden (1966, p 180), which has three sign-changes. This implies the real part of all characteristic roots to be positive. The bifurcation is a Hopf bifurcation and strong resonances are excluded. The stability criterion (20) follows from direct substitution in (29).

We continue by checking the transversality condition with respect to M_0 . The left-hand side of (20) is constant with respect to M_0 and greater than one (Lemma 4.3). The second term of the right-hand side is strictly decreasing (consider its reciprocal). We write the first term as

$$\frac{2 + \mathcal{M} - \mathcal{M}\hat{Z} - \mathcal{K}\hat{Z}}{1 + \mathcal{M}} = 1 + \frac{\exp(-\hat{Z})}{\kappa(\hat{Z})} \left(1 - \frac{M_1}{1 + \mathcal{M}}\right)$$

The above expression is strictly decreasing as long as it remains greater than one. It tends to one as \hat{Z} tends to infinity. It follows that equality occurs in (20) for a unique value of \hat{Z} . When equality occurs, the right-hand side of (20) has a strictly negative derivative with respect to \hat{Z} . Since \hat{Z} is an increasing function of M_0 , it follows from the chain rule that the right-hand side of (20) decreases with respect to M_0 when equality occurs. Thus, the transversality criterion of the Hopf bifurcation theorem holds. □

5. Numerical investigation of the food-chain model

We complete the above theoretical study with a numerical study. Our presentation to some extent follows the numerical study of a related model in Gyllenberg, Hanski, and Lindström (1996) and some of the methods are reminiscent of those used by Higgins, Hastings, and Botsford (1997).

The results for $M_1 = 1$, and $M_2 = 4$, appear quite typical and can be found in Figure 1, where a numerical comparison of the systems (5) and (7) was made. These parameter values satisfy (17) and (19) as long as $(\hat{X}, \hat{U}, \hat{Z})$ remains locally stable. The dynamics of the complete chain, (7), is represented by a solid line, while the corresponding dynamics of the carnivore-free system (5) is represented by a dotted line. The vertical dotted lines denote different regions of the parameter space, including those predicted by Lemma 3.2, Corollary 4.1, Theorem 4.2, and Theorem 4.4.

Region *A* denotes small values for the bifurcation parameter, M_0 . For such values the vegetation persists and is stable. Region *B* represents persistent and stable vegetation and herbivore populations. In region *C*, stable coexistence between all species is permitted. Between *C* and *D*, the Hopf bifurcation predicted

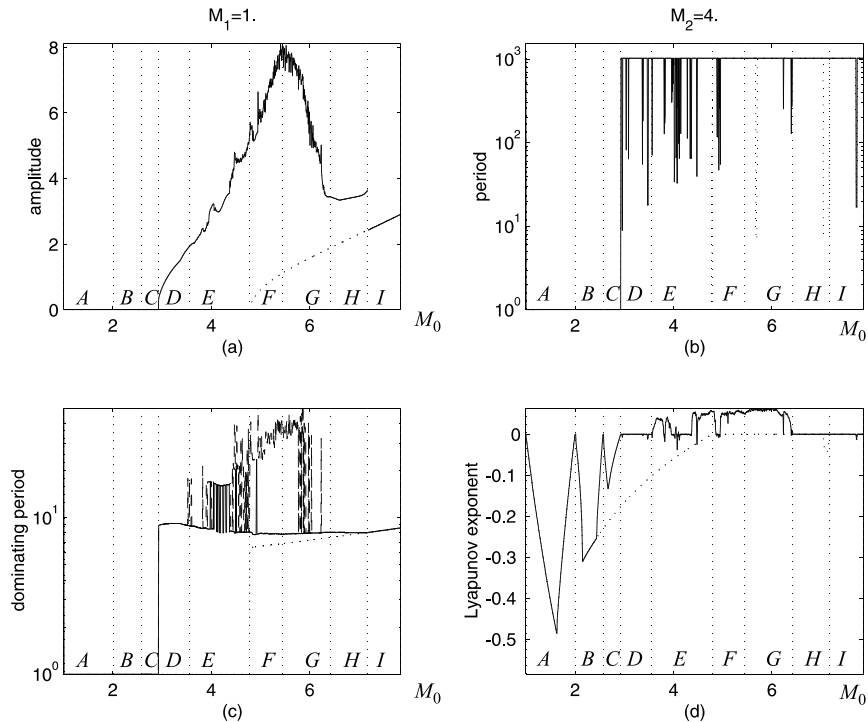


Fig. 1. Deterministic dynamics of the approximative food-chain model (7) (solid line) and the corresponding two-dimensional model (5) (dotted line) in different regions of the parameter space separated by dotted lines. (a) amplitudes. (b) periods. (c) dominating periods calculated from vegetation (solid) and the carnivores (dashed). (d) Lyapunov exponents.

by Theorem 4.4 occurs and D represents non-chaotic oscillatory coexistence. Figure 1(a) confirms that the mean-amplitude of the oscillations (measured in log-coordinates) grows parabolically in region D . Figure 1(c) shows a dominating period (period corresponding to the maximum of the Fourier-transform of the solution) larger than four, as predicted by Remark (a) after Theorem 4.4. At the end of region C a narrow region possessing alternative quasi- or high-periodic attractors may exist, see Remark (b) after Theorem 4.4. These attractors had approximately the same dominating periods as the those observed at the beginning of region D .

We should note that it makes no sense to separately discuss periods and Lyapunov exponents for various trophic levels. We have also chosen to measure amplitudes for the whole oscillation and not separately for the involved organisms, although in principle we could do that. On the other hand, in order to make a detailed study of the low- and high-frequency oscillations of the attractor in Figure 1(c), we separately calculated the dominating period of the vegetation time-series (solid line) and the carnivore time-series (dashed line).

Figures 2(b)-(c) illustrate typical cycles found in region D . These cycles start interacting with the saddle at $(M_0 - 1, 0, 0)$, denoted by a \circ mark, at even moderate values of M_0 above the Hopf bifurcation value. The points with highest- and lowest

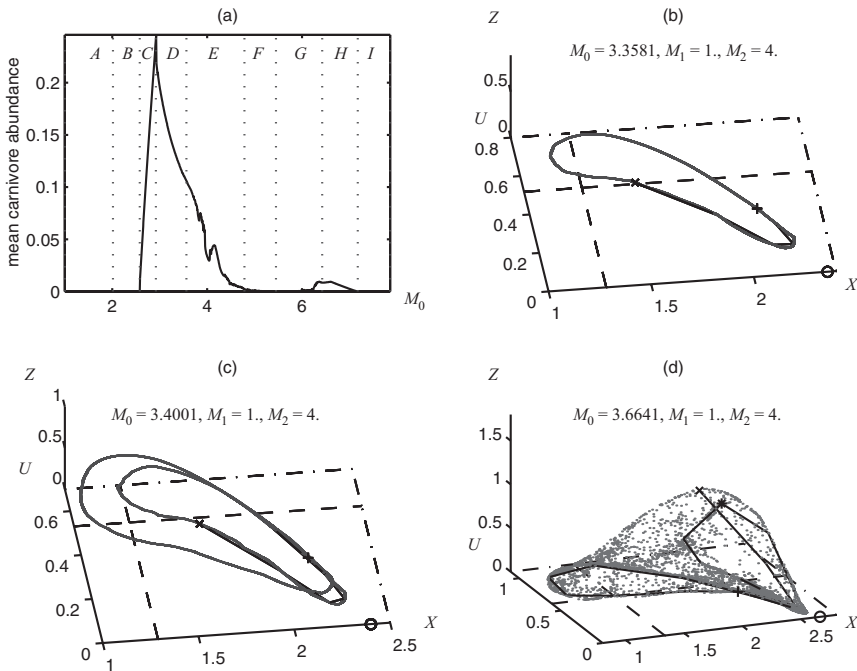


Fig. 2. (a) The mean deterministic carnivore abundance has a local optimum at the boundary of chaos and high-frequency cycles. (b) A quasiperiodic orbit is born in the Hopf bifurcation predicted by Theorem 4.4. (c) The quasiperiodic cycle has undergone transitions into a double cycle. (d) A book with cycles as pages pinched together in the vicinity of $(M_0 - 1, 0, 0)$ is formed.

Z elevation have been marked with \times and $+$ marks, respectively, and the orbit starting from the highest Z elevation has been denoted with a solid line until it reaches its first Z minimum. A typical feature of the attractors possessed by system (7), is that an abundant carnivore population crashes in the vicinity of the interval $(0, M_0 - 1)$ at the X -axis, which belongs to the stable manifold of $(M_0 - 1, 0, 0)$. After this, the carnivore population continues to decrease until it reaches its minimal value near the unstable manifold of $(M_0 - 1, 0, 0)$. This pattern is already visible at the parameter values indicated in Figure 2(b). As M_0 increases, this cycle becomes more and more complicated as Figure 2(c) indicates. Quite high-periodic solutions are usually involved in these transitions; for instance, we found both 55- and 183-periodic solutions for parameters representing values between those indicated in Figures 2(b)-(c).

A complicated transition to chaos is predicted to occur after the Hopf bifurcation, see Aronson et al. (1982). This transition involves quasiperiodic and periodic solutions. The pattern is confirmed by Figure 1(b), which gives the periods of the solutions (if any below 1024 were found). Note the difference between Figure 1(b) and 1(c). Figure 1(b) gives the exact period of the solutions (for instance in a period-doubling sequence such as 2, 4, 8, 16, etc.). Figure 1(c) gives the periods corresponding to the maximum of the Fourier-spectrum of the solution. These periods may correspond to non-integer values and are not always left invariant with respect to one-to-one coordinate transformations. Figure 1(d) gives the Lyapunov exponent, which remains close to zero throughout region D . The exact matching of detected periods in Figure 1(b) with evaluated negative Lyapunov exponents in Figure 1(d) was an important test for the global reliability of the used numerical representations of our system, see our comments after (8).

The transition to chaos is complete in region E , but it is questionable whether it can be reduced to occur in some two-dimensional invariant manifold as described by Aronson et al. (1982). We have illustrated a typical attractor found at the beginning of this region in Figure 2(d). One way to understand the structure of this attractor is to imagine it as a book with an infinite number of pages pinched together in the vicinity of $(M_0 - 1, 0, 0)$. Each page contains one cycle and each cycle contains a carnivore population crash. This feature is visible in Figure 1(c), since the dominant period of all population abundancies corresponds to the period born in the Hopf bifurcation. We have still marked the highest and lowest carnivore abundancies with \times and $+$ marks, respectively, and the crash from \times with a solid line. To illustrate the book-structure of the attractor we have also plotted another orbit with a solid line: this is the orbit through the carnivore crash with the highest vegetation abundancy, and it is marked with an $*$ mark. It forms the covers of the book-attractor.

As M_0 increases in region E , the attractor undergoes several changes before a tea-cup attractor (Hastings and Powell (1991)) is formed. Many stages have considerably simpler structures than the book- or the tea-cup attractors discussed here, and several high periodic forms are observed. For instance, in one of the periodic windows, our analysis revealed the period doubling sequence 34-68-136. However, the characteristic tea-cup structure is already clearly visible at the end of region E , that is, before the Hopf bifurcation predicted by Theorem 4.2 occurs. We have

illustrated such a tea-cup attractor in Figure 3(a). Its handle is formed by carnivore population crashes towards $(M_0 - 1, 0, 0)$, as the crash from the highest carnivore abundance shows. After the crash a period of vegetation-herbivore cycles occurs and carnivore abundance increases slowly. Therefore, the tea-cup attractor can be considered as a hybrid of high-frequency vegetation-herbivore cycles and low-frequency carnivore cycles.

The emerging hybrid-property in region E is also visible in Figure 1(c). At the beginning of region E , the vegetation time-series (solid line) and the carnivore time-series (dashed line) take dominating periods close to the period observed directly after the Hopf bifurcation in region D . In the end of region E the dominating period of the vegetation time-series is unchanged, while the carnivore time-series fluctuates with a clearly longer period.

The Hopf bifurcation predicted by Theorem 4.2 occurs at the boundary between regions E and F . The dominating period described by the emerging oscillations of (5) is marked by a dotted line in Figure 1(c), and does not stay far from the dominating period of the vegetation time-series. The characteristic patterns in region

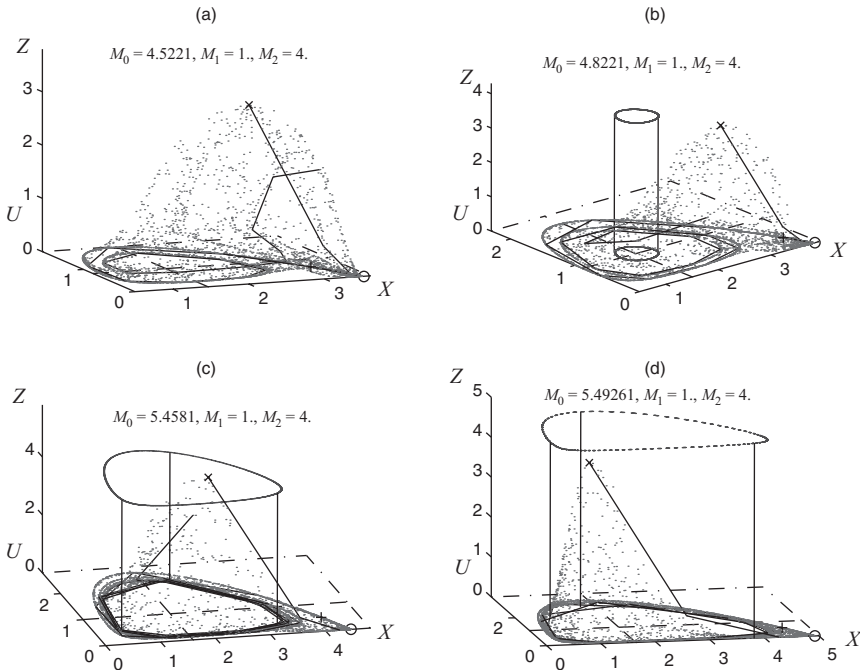


Fig. 3. (a) The tea-cup attractor is already formed in region E . (b) The Hopf bifurcation predicted by Theorem 4.2 forms an invariant cycle in the XU plane. (c) The invariant cycle in the XU plane grows larger, which decreases the geometric mean (cf. left-hand side of (9)) of the grazer population in the absence of carnivores. Larger and larger carnivore population crashes occur, which decreases their mean density. (d) The geometric mean of the grazer population in the absence of carnivores has become so small that it limits the crashes of the carnivore population. Mean carnivore abundance increases again and reaches a second top.

F are an increasing dominating period in the carnivore time-series (dashed line in Figure 1(c)) and an increasing mean amplitude of the oscillations (solid line in Figure 1(a)). Another characteristic feature is a falling mean carnivore abundance, see Figure 2(a), which does not fall because of nutrient scarcity. Instead, it is a consequence of the increasing amplitudes, which make the population remain at low densities for longer periods. We have illustrated a typical attractor found here in Figure 3(b). We have made visible the quasiperiodic oscillation representing the system (5) by lifting it slightly above its normal position in the XU plane. Also, here we marked an orbit starting from the highest carnivore abundance. The stable and unstable manifolds of the saddle $(M_0 - 1, 0, 0)$ still play the same role as before; but now it is clearly visible that the solution winds around the unstable manifold of the oscillations of (5).

The amplitude of the oscillations, Figure 1(a), reaches its maximum between F and G ; simultaneously the mean carnivore density reaches a local minimum, Figure 2(a). At this point the oscillations of the vegetation-herbivore system (5) have grown so large that the geometric mean of the herbivore density (cf. left-hand side of (9)) starts limiting the oscillations of the carnivores. The attractor at the boundary between region F and G (cf. Figure 3(c)) still has a tea-cup structure, but its handle is not more as vertical as in the end of region E . The carnivore crashes merely select a point between and $(0, 0, 0)$ and $(M_0 - 1, 0, 0)$ than the point $(M_0 - 1, 0, 0)$. This feature is even more dominant for parameter values in region G , see Figure 3(d), where the top of the tea-cup attractor is located almost above the origin.

In region G the mean carnivore abundance increases until the oscillations of (5) grow so large that they also start limiting the mean carnivore abundance and not just the oscillations. Consequently, we get a second local maximum for the mean carnivore abundance at the boundary between the regions G and H . At this point the oscillations of the complete system (7) have become quite reminiscent of the oscillations of (5), the carnivore-induced chaos disappears, see Figure 1(d), and we get herbivore-vegetation cycles with co-oscillating carnivores. According to our numerical results, Lemma 3.2 prevents carnivores from persisting in region I . For parameter-values far beyond those interesting in the three-dimensional case and moderate values of M_2 , the two-dimensional oscillations undergo a transition to chaos, see Aronson et al. (1982). Thus, for all parameter values included in our study, the boundary between chaos and non-chaos produces the optimizing properties described by De Feo and Rinaldi (1997).

Simultaneously, our result opens up possibilities for seeing under what conditions this result might be contradicted. According to our experiments, very high values of M_2 must be used to demonstrate such violations. The transition from stable to oscillating dynamics would not be described by Theorem 4.4 in this case, but it could be a matter for a subsequent study. Since the transition to chaos of (5) normally includes multiple attractors, the region is also interesting with respect to carnivore invasion (cf. our comments regarding Lemma 3.2).

Figure 4 illustrates the above patterns in the three-dimensional parameter space (M_0, M_1, M_2) . If $M_2 = 0$ the system (7) is fully described by the two-parameter system (5) (Lemma 3.2). Figure 4(a) gives a description of (5) in the parameter plane (M_0, M_1) . Herbivore extinction is indicated by green dots, locally stable

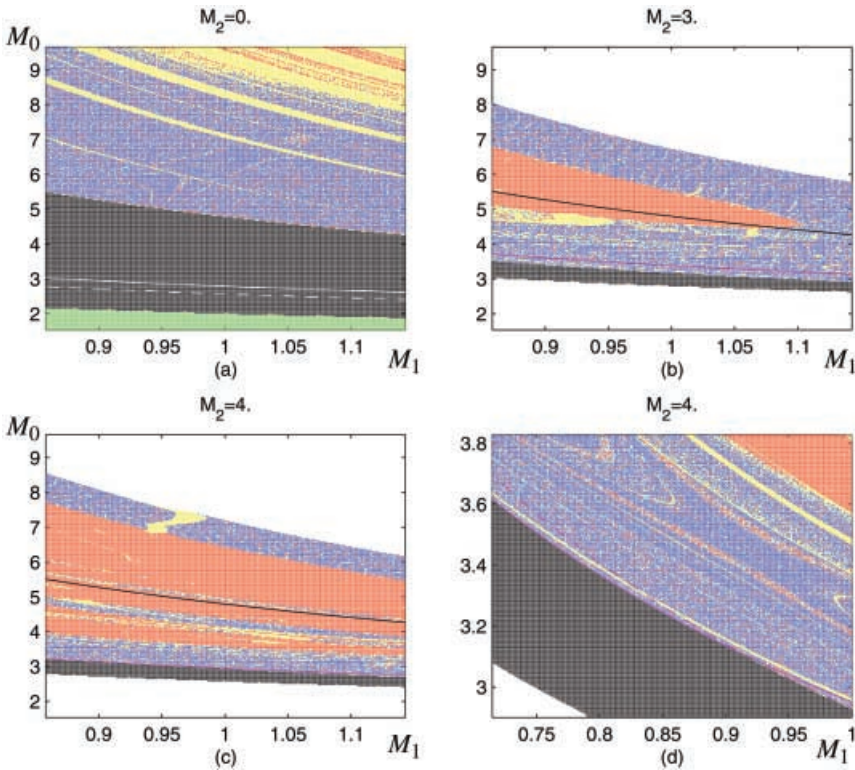


Fig. 4. Deterministic dynamics of the approximate food-chain model (7). In (a), the dynamics of (5) is given in the (M_1, M_0) plane as follows: Green dots represent dynamics governed by the fixed point $(M_0 - 1, 0, 0)$; black dots, locally stable coexistence; yellow dots, low-periodic solutions; light blue dots, high-periodic solutions where no period below 1024 was found; blue dots, quasiperiodic or bifurcating solutions; and finally red dots represent chaotic solutions. Note that this is model (7) with $M_2 = 0$ as indicated above the figure. In (b) the region affected by carnivore invasion at $M_2 = 3$, is plotted, and the corresponding solutions are given as in (a). In (c) the region affected at $M_2 = 4$, is presented in the same way, while (d) gives details of (c) close to the applicability range of Theorem 4.4.

coexistence by black dots, low-periodic solutions by yellow dots, high-periodic solutions by light blue dots, and quasi-periodic or bifurcating solutions by blue dots. Finally, red dots denote chaotic solutions.

When $M_2 \neq 0$, certain areas of the parameter plane in Figure 4(a) are affected by carnivore invasion. The lower bound of these areas is determined by the equality corresponding to (11). A white line in Figure 4(a) demonstrates this boundary in the cases $M_2 = 3$. (solid) and $M_2 = 4$. (dashed). The areas above these boundaries are partially affected by carnivore invasion, and the areas affected have been plotted in Figure 4(b) and Figure 4(c) for $M_2 = 3$. and $M_2 = 4$., respectively.

As a reference, the boundary between the locally stable and oscillating solutions in Figure 4(a) has been denoted by a black line in Figures 4(b)-(c). This line corresponds to the bifurcation predicted by Theorem 4.2 and to substantially higher

values of M_0 than the transition between locally stable and oscillatory solutions predicted by Figures 4(b)-(c). This is in concordance with our expectation that the implication (20) \Rightarrow (12) should be valid under general conditions, and shows that carnivore invasion is expected to destabilize the dynamics of (7), see Remark (d) after Theorem 4.4.

To check the applicability range of Theorem 4.4, we also plotted a purple line in Figures 4(b)-(c). This denotes the maximal M_0 for which (17) holds. We see that Theorem 4.4 contains enough information to describe the transition from locally stable to oscillatory dynamics when $M_2 = 3$, for all values of M_1 used in Figure 4(b). The applicability range of Theorem 4.4 is not that clear in the case $M_2 = 4$. (Figure 4(c)). We enlarged the critical parts of this case in Figure 4(d). We also denoted the transition between locally stable and oscillating dynamics as predicted by (20) with a dashed purple line. The dashed line intersects the solid line at approximately $(M_0, M_1) = (3.1056, .91501)$. Thus, the transition from locally stable to oscillating dynamics with enrichment is no longer described by Theorem 4.4 as $M_1 < .91501$ when $M_2 = 4.0$.

6. Summary

In this paper we have derived and analyzed qualitatively a discrete model for a food chain. Our qualitative analysis divides the parameter space roughly into nine different regions with respect to carrying capacity: persistence of the lowest trophic level (*A*), stable coexistence of vegetation and herbivores (*B*), stable coexistence of all three species possible (*C*), carnivore oscillations (*D*), carnivore oscillations interacting with stable herbivore-vegetation dynamics (*E*), increasing low-frequency carnivore oscillations interacting with high-frequency herbivore-vegetation oscillations (*F*), decreasing carnivore oscillations (*G*), herbivore-vegetation oscillations with co-oscillating carnivores (*H*), and pure herbivore-vegetation oscillations (*I*). Some of these stages may be attenuated or omitted (put for instance $M_1 > 1.1$ in Figure 4 (b)). Our analysis confirms the assertion of De Feo and Rinaldi (1997) that the mean carnivore-density is expected to have a local maximum at the boundary of chaos. It shows also how violations of this principle may arise.

We do not insist that all scenarios possible in continuous food chains displaying saturation effects can be reflected by this system. First, we were unable to detect cases where an invading carnivore can stabilize an oscillating herbivore-vegetation system, and conjecture that this holds true in the case (7). In contrast, discrete food chains with non-contest type competition at the lowest trophic level (Beddington and Hammond (1977)) can possess both stabilizing and destabilizing invading carnivores. Our observation stands in contrast to the stabilizing pattern Freedman and Waltman (1977) and Oksanen et al. (1981) found in continuous food chains. This might be due to a stabilizing property of unsaturated carnivores that is absent in discrete systems. We conjecture that observations of similar stabilizing patterns can be explained by generalist grazers/predators in food chains related to our system (see below).

Second, a difference noted in Sections 1 and 3 was that a continuous food chain with saturation effects can produce two equilibria allowing co-existence between

all involved species for certain parameter-values, while our food chain yields at most one such equilibrium. We think that this difference is non-essential for two reasons. First, the second equilibrium is always unstable if it exists, and hence not present in the visible dynamics of the continuous food chain. Second, conditions that guarantee two positive equilibria in a continuous food chain put a number of constraints on the parameters involved so that several conditions are to be met simultaneously (cf. Kuznetsov, De Feo, and Rinaldi (2001)). The presence of more parameters in the continuous model could therefore be one reason why our discrete model cannot reproduce all phenomena that have been reported in the continuous case.

The above division of the parameter space has the advantage that we know the trophic level and mechanism underlying the observations. In region *D-E* the system (7) possesses oscillating dynamics, while the system (5) possesses stable dynamics. Hence, we say that the oscillations and possible chaos in region *E* are caused by carnivores. A similar comparison between the systems (3), (5), and (7) in regions *F-G* leads to the conclusion that the oscillations can be caused by either herbivores or carnivores, but possible chaos is caused by the carnivores. The same holds for possible low-frequency behavior in addition to high-frequency behavior. Carnivores exist in region *H*, but their impact on the observed dynamics is negligible; the observed oscillations can almost be described through herbivore-vegetation interaction. In region *I* all observed oscillations are caused by herbivores. Behind region *I* herbivore-induced chaos may also occur.

Most difficulties should occur when distinguishing between regions *D* and *H*. In both cases the systems have persistent carnivore populations and no low-frequency behavior revealing the impact of carnivores. The system possesses periods of approximately the same frequency in both regions. These two cases respond, however, very differently to both carnivore-removal and enrichment. In region *D* the dynamics become more unpredictable through enrichment, and stable through carnivore removal. In region *H* enrichment will eliminate the carnivores while carnivore removal will not change the dynamics significantly.

An ecologist's obvious question is whether any of the observed patterns are observable when studying time series having their origin in food-chain systems. We need to realize that there are several problems connected to linking time-series data with these results. First, any time-series having its origin in real observations must be of finite length. Any attempt to gain an understanding of a complete food chain through time-series analysis will therefore face the difficulty of having only a few data points, if any, describing how carnivore crashes influence the system.

Second, from an evolutionary point of view the destabilizing features of the higher trophic levels reported here might produce niches for invading generalist predators/grazers that enter the system and cause a stabilizing effect for higher enrichment levels (cf. Hanski, Hansson, and Henttonen (1991); Lindström (1993)). Evolution, and the subsequent invasion of generalists could, for instance, remove the extinction boundary between regions *H* and *I*, thus making patterns that are part of the explanation invisible to the observer. Similar consequences of evolution have been reported by Gyllenberg, Hanski, and Lindström (1998).

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