Available online at www.sciencedirect.com
ScienceDirect
Mathematical Biosciences 210 (2007) 378–394
Mathematical Biosciences
www.elsevier.com/locate/mbs

A new class of non-linear stochastic population models with mass conservation ☆

S.A.L.M. Kooijman [a,*], J. Grasman [b], B.W. Kooi [a]

[a] *Department of Theoretical Biology, Vrije Universiteit, de Boelelaan 1087, 1081 HV Amsterdam, The Netherlands*
[b] *Mathematical and Statistical Methods Group, Wageningen University, Bornesesteeg 47, 6708 PD Wageningen, The Netherlands*

Received 11 January 2007; received in revised form 15 May 2007; accepted 18 May 2007
Available online 20 June 2007

Abstract

We study the effects of random feeding, growing and dying in a closed nutrient-limited producer/consumer system, in which nutrient is fully conserved, not only in the mean, but, most importantly, also across random events. More specifically, we relate these random effects to the closest deterministic models, and evaluate the importance of the various times scales that are involved. These stochastic models differ from deterministic ones not only in stochasticity, but they also have more details that involve shorter times scales. We tried to separate the effects of more detail from that of stochasticity. The producers have (nutrient) reserve and (body) structure, and so a variable chemical composition. The consumers have only structure, so a constant chemical composition. The conversion efficiency from producer to consumer, therefore, varies. The consumers use reserve and structure of the producers as complementary compounds, following the rules of Dynamic Energy Budget theory. Consumers die at constant specific rate and decompose instantaneously. Stochasticity is incorporated in the behaviour of the consumers, where the switches to handling and searching, as well as dying are Poissonian point events. We show that the stochastic model has one parameter more than the deterministic formulation without time scale separation for conversions between searching and handling consumers, which itself has one parameter more than the deterministic formulation with time scale separation for these conversions. These extra parameters are the contributions of a single

☆ More information about the DEB research program and its results can be found at http://www.bio.vu.nl/thb/deb/. You can download the software package DEBtool and use it to analyse the system dynamics numerically.

* Corresponding author.
E-mail address: bas@bio.vu.nl (S.A.L.M. Kooijman).
URL: http://www.bio.vu.nl/thb/ (S.A.L.M. Kooijman).

0025-5564/$ - see front matter
doi:10.1016/j.mbs.2007.05.010

individual producer and consumer to their densities, and the ratio of the two, respectively. The tendency to oscillate increases with the number of parameters. The focus bifurcation point has more relevance for the asymptotic behaviour of the stochastic model than the Hopf bifurcation point, since a randomly perturbed damped oscillation exhibits a behaviour similar to that of the stochastic limit cycle particularly near this bifurcation point. For total nutrient values below the focus bifurcation point, the system gradually becomes more confined to the direct neighbourhood of the isocline for which the producers do not change.

Keywords: Stochastic producer–consumer models; Nutrient conservation; Dynamic Energy Budget theory; Bifurcation theory

1. Introduction

Most models of interaction between two trophic levels, such as plant–herbivore or prey–predator systems are deterministic and do not keep track of the nutrient flow. Such systems are open and imply a hidden inflow of nutrients and/or energy. Hidden assumptions degrade the role of models in research. Another general problem is that biological phenomena have dynamical behaviour that is intrinsically erratic, and most concisely described by stochastic models, rather than by deterministic ones. While (bio)chemical transformations have a relatively high degree of predictability, the behaviour of individual organisms is much less predictable. The realistic description of this behaviour, including functional aspects, mass and energy conservation and the like, is far from easy, and basically multivariate. The nutrients and biomasses change in a coherent way which creates mutual dependencies that complicate the analysis. Most stochastic differential equations do not conserve nutrient, which is a problem in nutrient limited producer–consumer systems. Most of such systems are nutrient limited in practice [1].

By changing the deterministic closed system presented in [2] into a stochastic model we remedy the problem mentioned above. Closed systems are easy to open by allowing import and export, but open systems are less easy to close. It delineates nutrient, producers and consumers; the nutrient recycles and dead biomass is assumed to mineralise quickly and completely. The model rests on a highly simplified version of the Dynamic Energy Budget theory [3] for the processes of uptake and use of resources by individuals in a physiologically realistic way, and treats populations as collections of individuals that interact in specified manners. It has rules for how compounds are taken up from the environment and are converted into one or more reserves, and how reserves (quantified as internal nutrients) are converted into structure (whole organism except reserve) that requires maintenance. For primary producers, the compounds that are taken up from the environment are nutrients (and light), but for consumers this is producer biomass with a variable composition, composed of reserves and structure.

In a next step we bring in more detail by splitting up the consumer population in producer-searching and producer-handling consumers. Since the time between transitions to and from these states strongly fluctuates, we now include stochasticity, which necessitates an individual-based formulation and distinguish stochastic effects from those resulting from the additional level of detail. We use Monte Carlo techniques to analyse the dynamic properties of the stochastic model, as well as analytic local approximations for the steady state behaviour [4,5].

The deterministic models are analysed using bifurcation theory for the asymptotic behaviour of differential equations [6–8]. The bifurcation points are calculated with the software packages AUTO [9] and Content [10]. Also here the asymptotic behaviour of the system exhibits a non-trivial relationship with the total amount of nutrient N in the system. Five intervals can be distinguished marked by the following points: $N_t < N_f < N_H < N_g$, see Fig. 3. Below the tangent bifurcation point N_t we have the stable trivial equilibrium of extinction. From there until the focus bifurcation point N_f we have bistability, a stable internal node type equilibrium and a trivial extinction equilibrium. Next this positive stable equilibrium changes from a node into a spiral sink. At the Hopf bifurcation point N_H the equilibrium gets unstable and a stable limit cycle emerges. At the homoclinic bifurcation point N_g the limit cycle merges with the equilibrium of an unstable branch. Beyond this bifurcation point the behaviour of the system always converges to the stable equilibrium of extinction.

Although realistic, the explicit treatment of reserve in the producers might seem to be a minor detail that complicates simple population models like these unnecessarily; see also [11]. Yet this detail turned out to have a substantial effect on the asymptotic behaviour of the model and is reason for the presence of both the tangent bifurcation point N_t and the homoclinic bifurcation point N_g [2]. We, therefore, include these nutritional aspects.

The next section starts to recapitulate the simplified specification of the deterministic model, followed by the specification of the deterministic model that is most close to the stochastic one. The following sections specify the stochastic model, and analyse the properties of the models. We end with a brief discussion of the results.

2. Deterministic dynamics

Section 2.1 describes the producer–consumer system of [2]; see Table 1 for the notation. It assumes that the conversions from searching to handling consumers, and back, is fast relative to the feeding and growth process, which means that the fraction of searching consumers changes in quasi steady state.

The environment in which the producers and consumers live is homogeneous, closed for mass, and of unit volume. We, therefore, do not distinguish between amounts and densities of biomass. A number of simplifying assumptions apply

- no maintenance or reserves of the consumers
- no maintenance or aging for the producers
- instantaneous decay of consumer's feces and dead corpus

These simplifications of the DEB theory amount to Droop's kinetics for the producers (with a very small half saturation constant, and a very large specific maximum uptake rate), and Monod's kinetics for the consumer [3]. The reserve compartment of DEB theory corresponds with the cell quota minus the subsistence quota of the Droop model, see [3], and follows the same kinetics. While the Droop model is empirical, for the reserve dynamics a mechanism is known [12]. The Monod's kinetics results from the DEB model as a limit for increasing reserve turnover rates, and decreasing maintenance costs. We assume that the consumer treats the reserve and structure

Table 1
List of frequently used symbols, with dimension and interpretation

symbol	dim	interpretation
t	t	Time
N	mol l^{-3}	Total nutrient in the system
K	mol l^{-3}	Half saturation constant
P, P_ε	mol l^{-3}	Producer density, increment -
C, C_s, C_h, C_ε	mol l^{-3}	Consumer density , searching -, handling -, increment -
m_N	mol mol^{-1}	Nutrient-reserve density of producer
Y_{ij}, y_{ij}	mol mol^{-1}	Yield of i on j, constant -
y^ε_{CP}	mol mol^{-1}	Size of consumer relative to producer: $C_\varepsilon/P_\varepsilon = \dot{k}/j_{Pm}$
n_{Ni}	mol mol^{-1}	Chemical index of nutrient in i
j_P, j_{Pm}	mol mol^{-1} t^{-1}	Specific assimilation rate, max -
$\dot{r}_i$	t^{-1}	Specific growth rate of i
$\dot{h}_C$	t^{-1}	Hazard rate of consumer
$\dot{k}_N$	t^{-1}	Reserve turnover rate
$\dot{k}$	t^{-1}	Handling rate
δ_t	–	Scaled yield $\delta_t = 1 + Y_{CP}/y^\varepsilon_{CP}$
f	–	Probability density function for scaled state variables

The dots above symbols stand for the dimension "per time", and have nothing to do with differentiation. The dimension "mol" stands for mole of C-mole; the latter quantifies biomass in terms of carbon.

of the producer as complementary compounds. There exists considerable experimental support for the fact that the conversion of producer to consumer depends on the nutrient content of the producers [13,14]. The expression for the growth rate follows from the Synthesising Units (SUs) kinetics [15,16].

Next, in Section 2.2 we remove the time-scale separation of the conversions between searching and handling consumers, and deal explicitly with changes in these two subpopulations. The reason is to come as close as possible to the stochastic model. It appears that this partitioning not only introduces an extra differential equation, but also a new parameter: the ratio of the sizes of producer and consumer individuals.

2.1. Model with time-scale separation: TS-model

For simplicity's sake we first have a look at the formulation where the fraction of searching consumers changes in quasi steady state. In other words, we use the argument of time scale separation for this fraction, as done in most population models. The next subsection specifies in more detail how this fraction changes in time, and why it leads to the familiar Holling type II functional response. We work in an environment of unit volume, and don't distinguish between amounts or concentrations/densities.

Since the producers take up nutrient from the environment fast and efficiently, the free nutrient in the environment can be neglected, and the nutrient is in the structure of the consumers, or in that of the producers or in the reserve of the producers. Producer's reserve density m_N is obtained from the conservation of nutrient in the system

$$m_N(t) = N/P(t) - n_{NC}C(t)/P(t) - n_{NP} \tag{1}$$

for a total constant amount of nutrient N in the system, while the amounts of producers P and consumers C can change in time. The chemical indices n_{NP} and n_{NC} stand for producers' and consumers' nutrient content per carbon and are constant as well. This means that $P(t) \in (0, N/n_{NP})$ and $C(t) \in [0, N/n_{NC})$.

Following [16], the change in the amounts of producers $P(t)$ and consumers $C(t)$ is given by

$$\frac{\mathrm{d}}{\mathrm{d}t}P = \dot{r}_P P - j_P C \quad \text{with } \dot{r}_P = \frac{\dot{k}_N m_N}{y_{NP} + m_N} \text{ and } j_P = \frac{j_{Pm} P}{K + P} \tag{2}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}C = (\dot{r}_C - \dot{h}_C)C \quad \text{with } \dot{r}_C = (\dot{r}_{CP}^{-1} + \dot{r}_{CN}^{-1} - (\dot{r}_{CP} + \dot{r}_{CN})^{-1})^{-1} \tag{3}$$

$$\dot{r}_{CP} = y_{CP} j_P \quad \text{and } \dot{r}_{CN} = y_{CN} m_N j_P$$

where the specific growth rate of the producers $\dot{r}_P$ follows from Droop-kinetics and the specific feeding rate j_P is the hyperbolic functional response. The specific growth rate $\dot{r}_C$ of the consumers results from the standard SU rules for the parallel processing of complementary compounds (here producer's reserve and structure). The flux $\dot{r}_{CP}$ represents the contribution of the producer's structure to consumer's growth, and $\dot{r}_{CN}$ that of producer's reserve, while both compounds are required in the fixed stoichiometric ratio y_{CP}/y_{CN}.

If the conversion of reserve to structure in the producer is 100% efficient in terms of nutrients, we have that $y_{NP} = n_{NP}$, but typically we expect that $y_{NP} > n_{NP}$. The producers' reserve turnover rate is $\dot{k}_N$, and producers' maintenance is neglected.

The consumer has a constant hazard rate $\dot{h}_C$; dead consumers mineralise instantaneously, and the released nutrients are instantaneously taken up by the producers to become reserve.

Together with the initial conditions $P(0)$ and $C(0)$, the dynamics of our simple closed system is fully specified by Eqs. (1)–(3), which we will call the TS-model (time-scale separation model). These two initial values have to satisfy the condition $m_N(0) \geqslant 0$ in Eq. (1) in order to have a biologically meaningful formulation. Furthermore, it is easy to show that $m_N(0) \geqslant 0$ implies $m_N(t) \geqslant 0$ for $t > 0$.

2.2. Model with no time-scale separation: NTS-model

In preparation to the stochastic formulation we now refrain from application of the time-scale separation argument for the conversions between searching and handling consumers that is behind the hyperbolic functional response; the fraction of searching consumers no longer changes in quasi steady state. We do this by bringing in more detail from the individual level by delineating a feeding event at the association between a producer and a searching consumer. A searching consumer then converts into a handling consumer; the density of searching consumers decreases with one, while that of the handling consumers increase with one plus a contribution at the account of the digested producer. The handling consumer does not feed and converts back into a searching consumer with a constant specific flux $\dot{k}$. The handling period not only includes time invested in the mechanical aspects of feeding, but also chemical transformation work in digestion and conversion. The implementation of these details requires a partitioning of the consumers $C = C_s + C_h$ into searching C_s and food-handling C_h subpopulations.

Let P_ε denote the contribution of a single individual producer to the producer density P, and C_ε that of a single individual consumer to the consumer density C. We will need the coefficient $y^\varepsilon_{PC} = P_\varepsilon/C_\varepsilon = 1/y^\varepsilon_{CP}$ with the interpretation of the ratio of the amounts of structure of an individual producer and consumer, expressed in C-moles.

The rate at which C_s converts to C_h equals $\frac{\mathrm{d}}{\mathrm{d}t}C_s = -PC_s\dot{b}$, where $\dot{b}$ represents the encountering rate. Feeding is linked to this conversion and the rate amounts to $-\frac{\mathrm{d}}{\mathrm{d}t}P = PC_s\dot{b}y^\varepsilon_{PC}$, where y^ε_{PC} represents the conversion efficiency (= yield coefficient). The rate at which C_h converts to C_s equals $\frac{\mathrm{d}}{\mathrm{d}t}C_h = -\dot{k}C_h$, where $\dot{k}$ is the handling rate.

At the fast time scale, the change in the fraction of searching consumers $\theta_s = 1 - \theta_h$ is

$$\frac{\mathrm{d}}{\mathrm{d}t}\theta_s = \dot{k}\theta_h - \dot{b}P\theta_s = \dot{k} - (\dot{k} + \dot{b}P)\theta_s$$

The TS-model of the previous subsection assumes that the fraction θ_s changes in quasi steady state: $\theta^*_s = \frac{\dot{k}}{\dot{k}+\dot{b}P}$. The feeding rate $j_P C$ amounts to $\dot{b}P\theta^*_s C$ with half saturation constant $K = \dot{k}/\dot{b}$ and maximum specific feeding rate $j_{Pm} = y^\varepsilon_{PC}\dot{k}$. The feeding rate equals $PC_s j_{Pm}/K$.

The NTS-model, on the contrary, does not make the quasi steady state assumption, with the consequence that the parameters K, $\dot{k}$ and y^ε_{PC} are all independent, while the last two parameters only occur together in j_{Pm} in the TS-model. The time scale separation is the reason why the TS model has one parameter less than the NTS model. The encountering rate $\dot{b}$ only occurs in the easier-to-measure half saturation constant K in both models; $\dot{b}$ only plays a role in the mechanisms behind the model.

The transformation from producer to consumer is the same for the TS and the NTS models, but for the TS-model we dealt with the specific growth rate of the consumers directly, while for the NTS-model we deal with the transformation of producer to consumer structure explicitly; it is just a matter of presentation in preparation to the individual level of the stochastic model. This transformation occurs with a variable yield coefficient of C on P, namely

$$Y_{CP} = \left(y_{CP}^{-1} + y_{CN}^{-1}m_N^{-1} - (y_{CP} + y_{CN}m_N)^{-1}\right)^{-1} = \dot{r}_C/j_P \tag{4}$$

which is modified by the time-varying reserve density m_N while the yield coefficients y_{CP} and y_{CN} are constant.

The increase of handling consumers equals the decrease of searching consumers plus the amount of newly-synthesised consumers, so $\frac{\mathrm{d}}{\mathrm{d}t}C_h = PC_s\delta_t\dot{k}/K$ for $\delta_t = 1 + Y_{CP}/y^\varepsilon_{CP}$, where index t just reminds that δ_t can vary in time, because Y_{CP} can.

The dynamics of the system now becomes

$$\frac{\mathrm{d}}{\mathrm{d}t}P = P(\dot{r}_P - C_s j_{Pm}/K) \tag{5}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}C_s = C_h\dot{k} - C_s(\dot{h}_C + P\dot{k}/K) \tag{6}$$

$$\frac{\mathrm{d}}{\mathrm{d}t}C_h = C_s P\delta_t\dot{k}/K - C_h(\dot{h}_C + \dot{k}) \tag{7}$$

The expressions for $\dot{r}_P$ and m_N remain unchanged. We will call the model Eqs. (1), (5)–(7) the NTS-model (no time-scale separation model). It has one extra parameter compared to the system Eqs. (1)–(3) with time-scale separation, namely either the turnover rate $\dot{k}$ of the handling

consumers or the body mass ratio y^{ε}_{PC}, which are linked to the existing parameter j_{Pm} as $j_{Pm} = y^{\varepsilon}_{PC}\dot{k}$. Moreover we have one extra initial condition, namely $C_s(0)$ and $C_h(0)$ as opposed to $C(0)$.

2.3. Reducing the NTS-model to the TS-model

When the size of individual producers shrinks, $P_\varepsilon \to 0$, and the encountering and handling rates of producers by consumers increase, $\dot{b}, \dot{k} \to \infty$, such that the maximum specific feeding rate j_{Pm} and the half saturation constant K remain constant, the NTS-model reduces to the TS-model; so the dynamics of $C = C_s + C_h$ as specified in Eqs. (6) and (7) reduces to Eq. (3), while Eq. (5) reduces to Eq. (2) for $C_s = \theta^*_s C$. So the TS-model can be seen as a special case of the NTS-model, where consumers feed on producer-soup. When, on the contrary, the size of the individual producers increases, their numbers decrease at a given total amount of nutrient in the system, and stochastic phenomena become more important. We will study the implications of this in the next sections.

3. Stochastic dynamics

The stochastic model describes the events feeding F, searching S and death D as Poissonian point processes. With the NTS-model extended with the above stochastic components Monte Carlo type of simulations are carried out in Section 3.2. Considering the diffusion limit of the stochastic process we analyse the dynamics of the process locally near the internal equilibrium, making use of the concept of local persistence. The results are presented in Section 3.3.

3.1. The S-model

At ingestion of a producer by a searching consumer the amount of producers and of searching consumers make a step down with a single individual and the amount of searching consumers makes a step up with a single individual plus the amount of consumer synthesised from a individual producer (as discussed before). The feeding cycle is completed when a handling consumer becomes a searching consumer.

At death of a consumer, the reserve density of the producers makes a step up, such that the total amount of nutrient remains constant. The searching and handling consumers have the same hazard rate $\dot{h}_C$.

The implementation of these events requires the notion of individuals (notably their number), and gives P_ε and C_ε an independent role. Since $C_\varepsilon/P_\varepsilon = y^{\varepsilon}_{CP} = \dot{k}/j_{Pm}$ this means an extension with one more parameter, relative to the NTS-model.

Table 2 gives the possible events F feeding, S searching, D_s dying of C_s and D_h dying of C_h, the intensities λ_i and the steps sizes at time t. The last process G, the growth of the producers, is supposed to be a deterministic continuous process, not a stochastic point process; the producers continue to grow between the Poissonian events, i.e. $\frac{\mathrm{d}}{\mathrm{d}t}\underline{P} = \dot{r}_P\underline{P}$ where the specific growth rate $\dot{r}_P$ is given in Eq. (2), producers' reserve density m_N changes as Eq. (1) and the (variable) yield Y_{CP} is given by Eq. (4). Between the stochastic jump events m_N, $\dot{r}_P$ and Y_{CP} change smoothly and deterministically, while the consumer densities C_s and C_h remain constant. At a time-incremental basis, $\underline{m}_N$, $\underline{\dot{r}}_P$ and $\underline{Y}_{CP}$

Table 2
The possible stochastic events F, S, D_s and D_h, the intensities $\dot{\lambda}_F$, $\dot{\lambda}_S$, $\dot{\lambda}_{D_s}$ and $\dot{\lambda}_{D_h}$ and the steps sizes ($\mathrm{d}P$, $\mathrm{d}C_s$, $\mathrm{d}C_h$), given the state (P, C_s, C_h) of the system at time t

Event type i intensity $\dot{\lambda}_i$	F feeding $\dot{k}\frac{PC_s}{KC_\varepsilon}$	S searching $\dot{k}\frac{C_h}{C_\varepsilon}$	D_s dying of C_s $\dot{h}_C\frac{C_s}{C_\varepsilon}$	D_h dying of C_h $\dot{h}_C\frac{C_h}{C_\varepsilon}$	G growing $\dot{r}_P\frac{P}{P_\varepsilon}$
Change					
$\mathrm{d}P$	$-P_\varepsilon$	0	0	0	P_ε
$\mathrm{d}C_s$	$-C_\varepsilon$	C_ε	$-C_\varepsilon$	0	0
$\mathrm{d}C_h$	$\underline{\delta}_t C_\varepsilon$	$-C_\varepsilon$	0	$-C_\varepsilon$	0

The growth process G is deterministic and continuous. Mass balance restrictions make that the steps in the three variables are coordinated. The coefficient δ_t varies in time, due to stoichiometric constraints on the growth of the consumers from structure as well as varying reserve of the producers. The system is closed for nutrient, so for producers and consumers as well, while nutrient uptake by the producers is large enough to cause negligibly small concentrations of free nutrient.

are stochastic, because they are functions of $\underline{P}$ and $\underline{C} = \underline{C}_s + \underline{C}_h$. Together with the initial conditions $P(0)$, $C_s(0)$ and $C_h(0)$, this fully specifies the stochastic dynamics, which we will call the S-model (stochastic model). Again we have the constraint $m_N(0) > 0$ on the initial conditions.

3.2. Numerical simulation

Since between the stochastic events the growth of producers increases continuously in a deterministic way, we cannot step from event to event with exponentially distributed time steps [17]. On the other hand using a forward Euler scheme with a fixed small time step would make the simulations highly time consuming. Therefore, the numerical method that we used for the simulations is a variable time step technique, where the time increment is such that an event of the fastest process occurs with probability 0.1. At the start of the interval, a random number generator is used for each possible type of event to decide whether or not a jump is made, followed by a numerical integration for the deterministic change of the producers, given the values of the consumers.

Fig. 1 presents the trajectory of the S-model where the total amount of nutrient is such that the equilibrium is stable and the system exhibits a damped oscillation. Although the start is at the equilibrium, stochastic effects cause deviations from this equilibrium and overshoot effects induce an irregular oscillatory behaviour.

3.3. Stationary pdf and its local approximation

We collect the state variables in vector $\boldsymbol{X} = (P, C_s, C_h)^{\mathrm{T}}$, and the changes in vector $\mathbf{d}\boldsymbol{X} = (\mathrm{d}P, \mathrm{d}C_s, \mathrm{d}C_h)^{\mathrm{T}}$. Let index $i \in \{F, S, D_s, D_h, G\}$ scan the five different processes. The expected change, given $\boldsymbol{X}(t)$, amounts to $\frac{\mathrm{d}}{\mathrm{d}t}\mathcal{E}\boldsymbol{X} = \sum_i \mathbf{d}X_i\dot{\lambda}_i$. This exactly corresponds to Eqs. (5)–(7), which can be rewritten as $\frac{\mathrm{d}}{\mathrm{d}t}\boldsymbol{X} = \dot{\boldsymbol{b}}(\boldsymbol{X})$, so $\mathcal{E}\Delta\underline{\boldsymbol{X}}|\boldsymbol{X} = \dot{\boldsymbol{b}}(\boldsymbol{X})\Delta t + O(\Delta t^2)$ with drift $\dot{\boldsymbol{b}}$ is the vector-valued function

$$\frac{\dot{\boldsymbol{b}}(\boldsymbol{X})}{\dot{k}} = \begin{pmatrix} \dot{r}_P/\dot{k} & -Py^{\varepsilon}_{PC}/K & 0 \\ 0 & -h - P/K & 1 \\ 0 & P\delta_t/K & -h-1 \end{pmatrix}\boldsymbol{X} \tag{8}$$

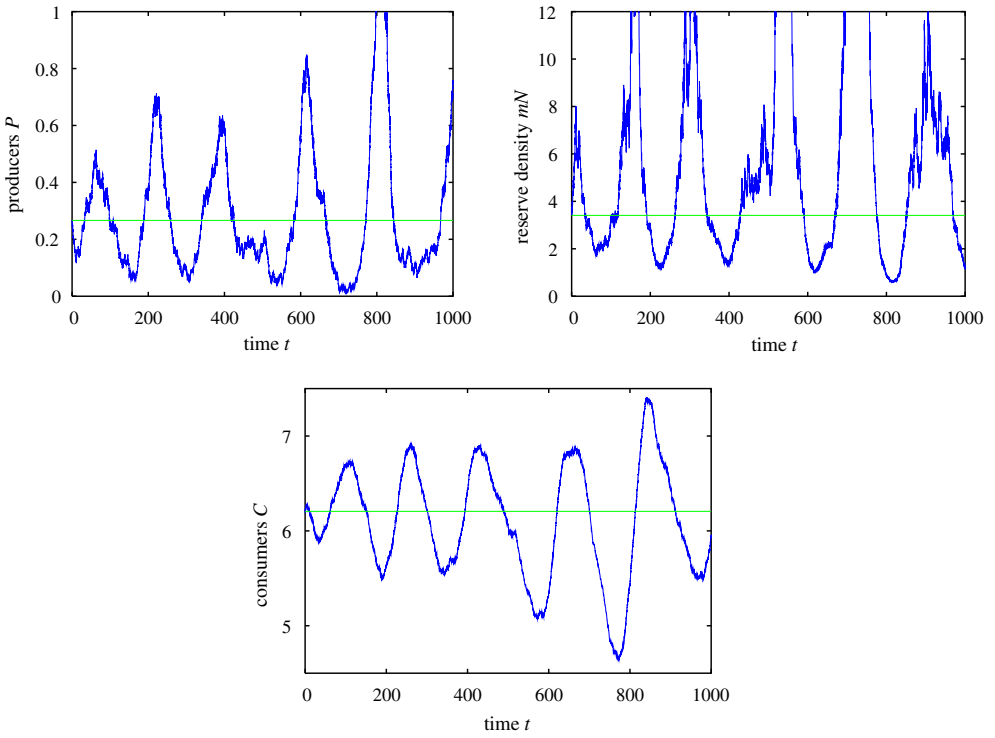

Fig. 1. The producer/consumer system for the S-model (dark), starting at the equilibrium of the NTS-model (grey). Parameter setting: $N = 2.5$ mM (which is between the focus and Hopf bifurcation points), $\dot{h}_C = .005\ \mathrm{h}^{-1}$, $K = 10$ mM, $j_{Pm} = .4\ \mathrm{h}^{-1}$, $n_{NP} = .15$, $n_{NC} = .25$, $y_{NP} = .15$, $y_{CN} = .8$, $y_{CP} = .5$, $\dot{k}_N = .25\ \mathrm{h}^{-1}$, $\dot{k} = .5\ \mathrm{h}^{-1}$, $P_\varepsilon = .005$ mM. We have $C_\varepsilon = P_\varepsilon \dot{k}/j_{Pm}$.

for $\delta_t = 1 + Y_{CP}/y^{\varepsilon}_{CP}$ and $h = \dot{h}_C/\dot{k}$. The variance-covariance matrix of the change in $\underline{\boldsymbol{X}}$ is $\mathrm{Cov}(\Delta\underline{\boldsymbol{X}}, \Delta\underline{\boldsymbol{X}}^T|\boldsymbol{X}) = \dot{\boldsymbol{a}}(\boldsymbol{X})\Delta t + O(\Delta t^2)$, where diffusion $\dot{\boldsymbol{a}}$ is the matrix-valued function

$$\frac{\dot{\boldsymbol{a}}(\boldsymbol{X})}{\dot{k}C_\varepsilon} = \frac{PC_s}{K}\begin{pmatrix} y^{\varepsilon 2}_{PC} & y^{\varepsilon}_{PC} & -y^{\varepsilon}_{PC}\delta_t \\ y^{\varepsilon}_{PC} & 1 & -\delta_t \\ -y^{\varepsilon}_{PC}\delta_t & -\delta_t & \delta_t^2 \end{pmatrix} + \begin{pmatrix} 0 & 0 & 0 \\ 0 & C_h + hC_s & -C_h \\ 0 & -C_h & (1+h)C_h \end{pmatrix} \tag{9}$$

Taking the diffusion limit we arrive at the probability density function f of $\boldsymbol{X}$ given by the forward Kolmogorov equation [4]

$$\frac{\partial}{\partial t} f = -\sum_{i=1}^{3} \frac{\partial}{\partial X_i}(\dot{b}_i(\boldsymbol{X})f) + \frac{1}{2}\sum_{i,j=1}^{3} \frac{\partial^2}{\partial X_i \partial X_j}(\dot{a}_{ij}(\boldsymbol{X})f) \tag{10}$$

The stationary distribution of $\boldsymbol{X}$ is found from $\frac{\partial}{\partial t} f = 0$. It can be approximated by solving an equation in which the drift and diffusion are approximated near the stable equilibrium $\boldsymbol{X}^*$ of the NTS model. We take a linear drift approximation and a constant diffusion

$$\dot{\boldsymbol{b}}(\boldsymbol{X}) \simeq \dot{\boldsymbol{B}}(\boldsymbol{X} - \boldsymbol{X}^*) \quad \text{and} \quad \dot{\boldsymbol{a}}(\boldsymbol{X}) = \dot{\boldsymbol{a}}(\boldsymbol{X}^*) = \dot{\boldsymbol{A}}$$

where $\dot{\boldsymbol{B}}$ is the Jacobian of $\dot{\boldsymbol{b}}(\boldsymbol{X})$ at $\boldsymbol{X} = \boldsymbol{X}^*$, i.e. $\dot{\boldsymbol{B}} = \frac{\mathrm{d}}{\mathrm{d}\boldsymbol{X}}\dot{\boldsymbol{b}}^{\mathrm{T}}(\boldsymbol{X}^*)$. Thus, locally the system behaves as an Ornstein-Uhlenbeck process [5] with a multivariate normal distribution as stationary solution. Its covariance matrix $\boldsymbol{S}$ satisfies the matrix equation

$$\dot{\boldsymbol{A}} + \dot{\boldsymbol{B}}\boldsymbol{S} + \boldsymbol{S}\dot{\boldsymbol{B}}^{\mathrm{T}} = 0$$

The 80% confidence ellipsoid in the $\boldsymbol{X}$-space with the equilibrium in the centre is given by

$$(\boldsymbol{X} - \boldsymbol{X}^*)^{\mathrm{T}}\boldsymbol{S}^{-1}(\boldsymbol{X} - \boldsymbol{X}^*) = \chi^2_{3,0.8}, \tag{11}$$

where $\chi^2_{3,0.8} = 4.641$ is the value for which the distribution function of the Chi-square distribution with 3 degrees of freedom equals 0.8. To construct the 80% confidence ellipse in the (P, C)-plane we carry out the transformation

$$\boldsymbol{Y} = \boldsymbol{M}(\boldsymbol{X} - \boldsymbol{X}^*) \quad \text{with } \boldsymbol{M} = \begin{pmatrix} 1 & 0 & 0 \\ 0 & 1 & 1 \end{pmatrix},$$

so that $\boldsymbol{Y}^{\mathrm{T}} = (P, C)$. Eq. (11) then becomes

$$\boldsymbol{Y}^{\mathrm{T}}(\boldsymbol{M}\boldsymbol{S}\boldsymbol{M}^{\mathrm{T}})^{-1}\boldsymbol{Y} = \chi^2_{2,0.8} \tag{12}$$

where $\chi^2_{2,0.8} = 3.219$. Fig. 2 illustrates the application with $P_\varepsilon = 0.005$.

In [18] the notion of local persistence was introduced. The smaller the maximal diameter of this ellipsoid the more the system persists close to this equilibrium state. The ellipsoid is determined by the variance–covariance matrix S.

4. Model properties

4.1. Total nutrient as bifurcation parameter

Three bifurcations play a key-role in our analysis of the deterministic models as functions of the total amount of nutrient: the tangent bifurcation and the Hopf bifurcation. In the tangent bifurcation point (T_e) one eigenvalue of the Jacobian of the vector field describing the rates of change in the corresponding deterministic system is zero, the other one (for the TS model) or two (for the

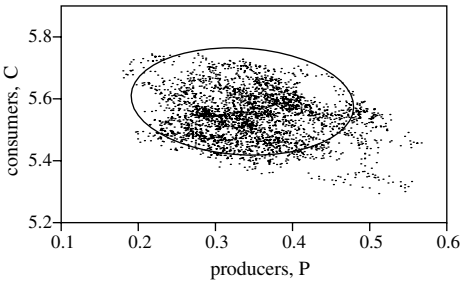

Fig. 2. Scatter diagram of (P, C) for $N = 1.75$ near the deterministically stable internal equilibrium. Due to the random perturbations the state variables fluctuate resulting in approximately a multivariate normal distribution. The 80% confidence ellipse is depicted.

NTS model) is/are negative. The tangent bifurcation marks the transition between zero and two positive equilibria. At the Hopf bifurcation point (H^-) of the TS model the real parts of two conjugated eigenvalues are zero. The third eigenvalue of NTS-model has a negative real part. The Hopf bifurcation marks the transition from a stable equilibrium to a limit cycle [19]. The homoclinic bifurcation point ($G^=$) marks the transition from a limit cycle to extinction.

For the study of the S-model a special point between the tangent and the Hopf bifurcation point appeared to be important, namely the focus bifurcation point. At this focus point two eigenvalues are equal and negative. It marks the transition between a stable node and a spiral sink. In the region between the tangent and the focus bifurcation the eigenvalues are real and negative, and in the region between the focus and the Hopf bifurcation they are complex and conjugated with negative real parts in the TS model. The NTS-model has three eigenvalues, the third one has a negative real part. The focus point is generally not considered to be a bifurcation point since the qualitative long-term dynamics of the deterministic system does not change when the bifurcation parameter crosses this point; in both cases there is convergence to the equilibrium point.

Fig. 3 presents the bifurcation diagram of the NTS model as a function of the total amount of nutrient N. The TS model has qualitatively similar behaviour compared to the NTS model, but the tangent bifurcation point is somewhat lower and the Hopf bifurcation point is somewhat larger than that of the NTS model. In the limiting case $y^e_{PC} \to 0$ or $\dot{k} \to \infty$ the critical values of the bifurcation parameter N for the tangent bifurcation T_e and supercritical Hopf bifurcation H^-

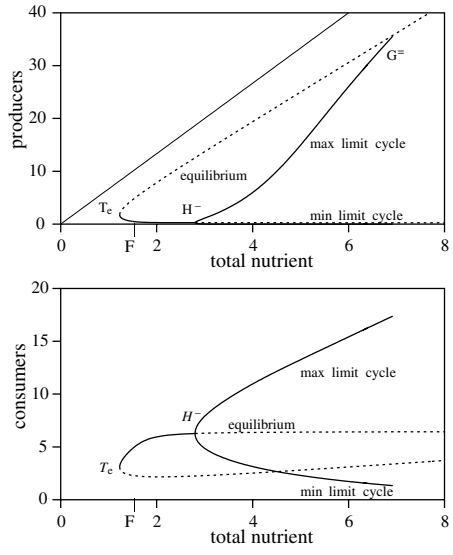

Fig. 3. The producer-consumer dynamics of the NTS-model. The bifurcation diagrams for the producer (top) and the consumer (bottom) are given, using the total amount of nutrient as bifurcation parameter. At very low nutrient levels, the system cannot exist; the stable equilibria with $P = N/n_{NP}$, $C = 0$ are also indicated. At intermediary nutrient levels, the system has a point attractor. A tangent (T_e) and a Hopf bifurcation point (H^-) mark the boundaries of these intermediary nutrient levels. At larger nutrient levels, the system oscillates with increasing amplitude. A homoclinic bifurcation point ($G^=$) marks the upper boundary of this interval; the system cannot exist at higher nutrient levels. The focus bifurcation point is indicated with F. Parameters: $\dot{h} = 0.005\ \mathrm{h}^{-1}$, $n_{NP} = 0.15\ \frac{\mathrm{mol}}{\mathrm{mol}}$, $n_{NC} = 0.25\ \frac{\mathrm{mol}}{\mathrm{mol}}$, $y_{CN} = 0.8\ \frac{\mathrm{mol}}{\mathrm{mol}}$, $y_{CP} = 0.5\ \frac{\mathrm{mol}}{\mathrm{mol}}$, $y_{NP} = 0.15\ \frac{\mathrm{mol}}{\mathrm{mol}}$, $K = 10$ mM, $j_{Pm} = 0.4\ \frac{\mathrm{mol}}{\mathrm{mol\ h}}$, $\dot{k}_N = 0.25\ \mathrm{h}^{-1}$, $y^e_{PC} = 0.8\ \frac{\mathrm{mol}}{\mathrm{mol}}$.

converge to their critical values in the TS-model. The range of N values for which a non-trivial point attractor for the TS model exists fully covers that of the NTS-model. See Table 3.

For $N \to \infty$, we have that $m_N \to \infty$, $\dot{r}_P \to \dot{k}_N$, $\dot{r}_{CN} \to \infty$, $\dot{r}_C \to \dot{r}_{CP} = y_{CP} j_P$, which gives the equilibrium values

$$P^* = \frac{K}{y_{CP} j_{Pm}/\dot{h}_C - 1}; \quad C^* = \frac{\dot{k}_N K}{j_{Pm} - \dot{h}_C/y_{CP}}; \quad \frac{C_s^*}{C^*} = \frac{1}{1 + P^*/K + \dot{h}_C/\dot{k}}$$

and holds for all three models (if we consider expected values for the stochastic model). Fig. 3 shows that the equilibrium is close to these values for $N > 2$, given the chosen parameters.

Fig. 4 gives simulations of a stochastic trajectory for various choices of the total nutrient, starting from the equilibrium of the NTS-model, or a random point on its limit cycle. We see that the S-model has the tendency to cycle for nutrient values N larger than the value at the focus bifurcation point [20], above this point the equilibrium behaves as a spiral sink. So the transient dynamics is of relevance for the stationary behaviour of the S-model. Stochastic effects bring the system out of its (deterministic) equilibrium inducing irregular cyclic behaviour. The higher the value of N the more visible this effect is because of the increasing variance in the local stationary solution (Fig. 5). The stochastic trajectories look more cyclic than we expected from the damped oscillation of the corresponding deterministic system. A further increase across the Hopf bifurcation point does not change the qualitative behaviour much although deterministically the equilibrium went over in a limit cycle. New is that for large N the trajectory gets periodically close to the plane $P = 0$. Extinction of the producers and a total collapse of the system is therefore then highly probable.

If N decreases below the focus bifurcation point, the scatter builds up along the isocline for which $\frac{\mathrm{d}}{\mathrm{d}t} P = 0$, see Fig. 4. If N decreases below the tangent bifurcation point ($N = 1.2296$) and starting on this isocline, the trajectory of the S-model becomes increasingly confined to this isocline. This isocline no longer intersects the isocline for which $\frac{\mathrm{d}}{\mathrm{d}t} C = 0$.

4.2. Local persistence at steady state

In Section 3.3 we derived a multi-variate normal distribution as local approximation of the stationary pdf near the equilibrium state. In Fig. 5 the square root of the variance, the maximum standard deviation, is depicted for the N-interval between the tangent and the Hopf bifurcation points, where the S-model has a stable equilibrium. This maximum variance is a measure for the local persistence of the system [18]; the minimum is in the region of the focus bifurcation point. As N approaches the bifurcation points where the equilibrium gets unstable, the maximum variance tends to infinity (possible loss of local persistence) due to the fact that the Jacobian of the

Table 3
The various bifurcation points for the total nutrient N in the case of the TS- and the NTS-model

	Tangent	Focus	Hopf	Global
TS	1.217	1.520	3.165	7.11
NTS	1.229	1.535	2.801	6.96

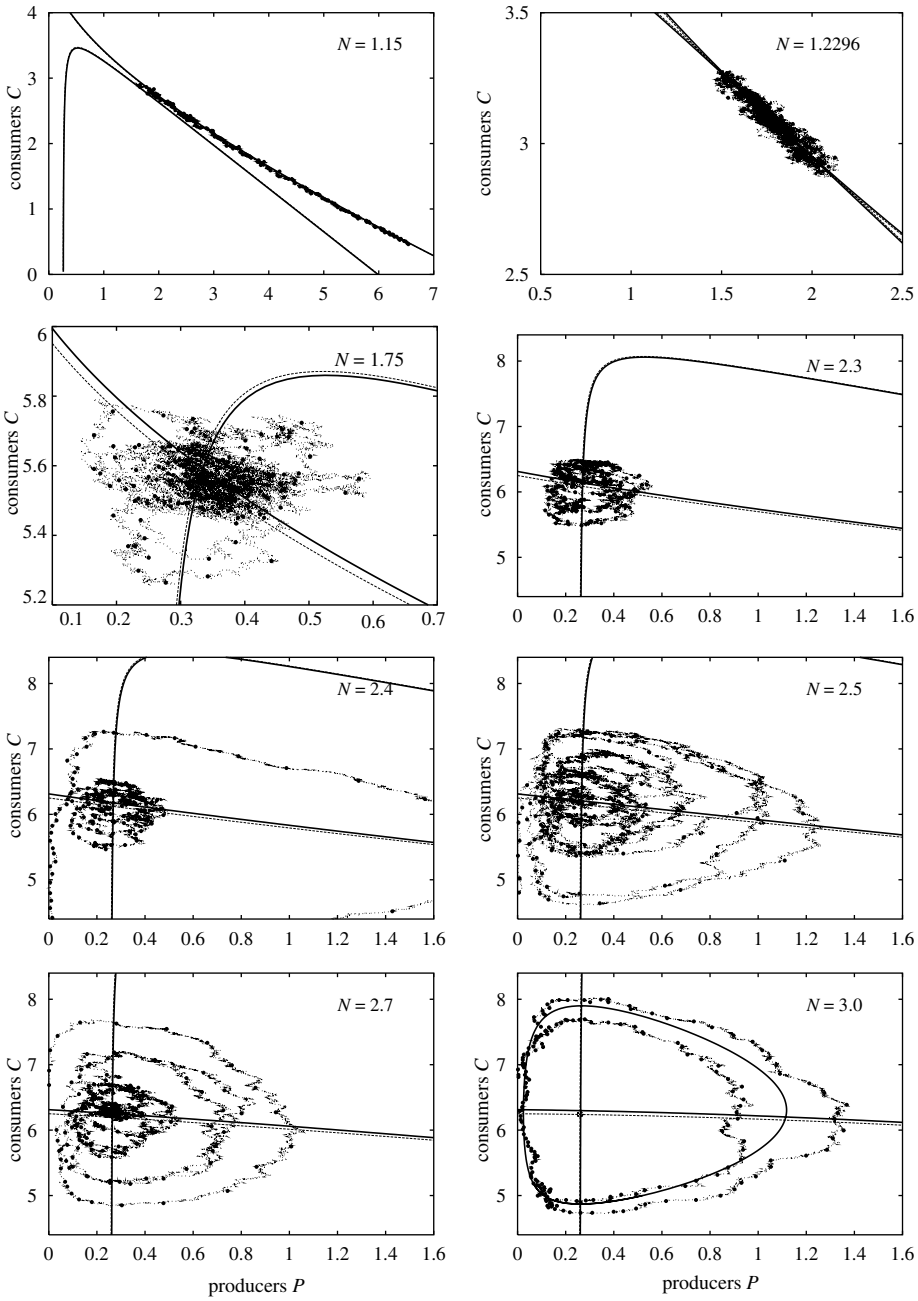

Fig. 4. The trajectory of the stochastic model for the parameter values of Fig. 1, but with different values for the total amount of nutrient N. The fat dots are the linearly interpolated values with equal time units apart. For low N-values, the start is at the stable equilibrium of the expected value of S-model, which is at the intersection of the $\frac{\mathrm{d}}{\mathrm{d}t}P = 0$ and the $\frac{\mathrm{d}}{\mathrm{d}t}C_h = 0$ isoclines (while $\frac{\mathrm{d}}{\mathrm{d}C_h}C_s = 0$; solid curves). For large N-values ($N = 2.7, 3.0$), the start is at a random point of the limit cycle of the NTS-model. The isoclines of the TS model are plotted as well (stippled). Notice that for $N = 2.3$ few points of the S-model are at the mean, because of its tendency to cycle. For $N < 2.6$ 1000 time units are used, and 5000 for $N > 2.6$.

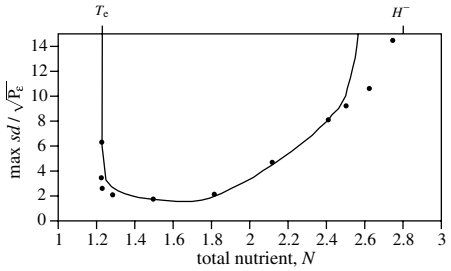

Fig. 5. The maximum standard deviation of the multivariate normal distribution approximating the quasi stationary solution near the stable equilibrium between the tangent (T_e) and the Hopf (H^-) bifurcation points. Near the Hopf bifurcation point the linearisation does not hold. This is also seen from the simulation results (dots). Still the variance remains bounded as there is a smooth transition to a limit cycle. At the bifurcation point at the tangent end of the interval the linear approximation also deviates from the simulation results, but now the variance gets unbounded because of the type of bifurcation (saddle-node).

deterministic system at the equilibrium has an eigenvalue of which the (negative) real part vanishes at the bifurcation points.

Near these points the analysis of local persistence based on the linearisation of the system does not hold; the simulation results do not coincide with the outcome of the analytical analysis (see Fig. 5). Repeating the simulations we observe a large variability in the maximal standard deviation at these points. Above the tangent bifurcation an unstable and a stable deterministic equilibrium exist close to each other. Furthermore, there is the stable trivial equilibrium of extinction. The separating manifold of the attraction domains of the two stable equilibria contains the unstable equilibrium. The stochastic dynamics shows a behaviour that is characteristic for non-linear randomly perturbed systems. It is likely that the system leaves the domain of attraction of the internal stable point for some time and it even may run away permanently in the direction of the point of extinction in the plane $P = 0$, see [21, p 209]. Below the bifurcation point the system slows down if it arrives in the region where the saddle-node bifurcation takes place. Then it accelerates and moves also in that case to the equilibrium with the producers being extinct.

At the Hopf bifurcation point there is a smooth transition to a limit cycle, so local persistence is not lost. Fig. 6 presents a scatter diagram for the consumers with N in the interval [1.8, 2.8], which further illustrates the increase in the variance in the stable region towards the Hopf bifurcation at

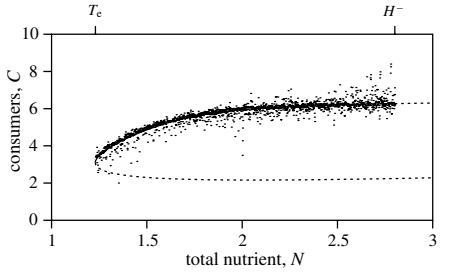

Fig. 6. The scatter diagram for the consumers as function of the total amount of nutrient, between the tangent and Hopf bifurcation points.

one end as well as to the tangent bifurcation at the other end. The figure is produced by starting with N at the tangent bifurcation point and by next slowly increasing its value. At the same time P_ε decreases linearly in order to illustrate the stochastic behaviour of the process over the full range of the parameter N as otherwise the stochastic effect becomes too strong so that extinction events take place for N below the Hopf bifurcation point. We took $P_\varepsilon = 0.145 - 0.05\ N$.

4.3. Global stochastic behaviour

A high total amount of nutrient ($N > 3$ in this case) induces cyclic behaviour with stages of very low values of producers and consumers as bottle-necks. This destabilising effect of nutrient enrichment is well known [21]. The S-model then easily leads to extinction so that the behaviour around the homoclinic bifurcation point is irrelevant for the S-model. The S-model is more realistic in this respect. At the other side of the range, for N below the tangent bifurcation, extinction also occurs in a short time as the system then tends to a boundary equilibrium. Extinction is less likely in the range of N-values where the deterministic system has a stable internal equilibrium. Theoretically the stochastic system leaves the domain of attraction of this point with probability one in finite time. This will lead to extinction of the producers [4]. The expected time needed to move from the stable equilibrium to the point of extinction is exponentially large with respect to P_ε^{-1} and has no consequences for the model within its present scope.

5. Discussion

We can state that the predicted dynamic behaviour of the S-model changes smoothly with the total amount of nutrient anywhere in its range, and that the focus bifurcation point is of more relevance for its asymptotic behaviour than the Hopf bifurcation point. This observation probably applies to the whole family of stochastic models of this type. We think that this family of stochastic models is more realistic than the corresponding deterministic models. The smooth change of properties of stochastic models as functions of the total amount of nutrient might explain the lack of empirical support for sharp changes in observed behaviour [22].

The stochastic population model differs from the corresponding deterministic one not only because it is stochastic, but also because it involves more properties at the individual level; this comes with extra parameters with a clear biological interpretation. We tried to separate the effects of stochasticity and that of more detail by removing a time scale separation argument that is behind the hyperbolic functional response. For this purpose we partitioned the consumer population in searching and handling consumers. We were able to reveal this detail by two new parameters compared to the original deterministic model, and by one new parameter compared to the nearest deterministic model. Individuals only play an explicit role in the stochastic model.

Because stochastic effects bring the system out of its deterministic equilibrium, the asymptotic behaviour has the tendency to cycle in situations where the corresponding deterministic system has a spiral sink to its point attractor. The producers can change faster than the consumers in this model (with the chosen parameter values), and the biggest scatter is along the P-isocline. Therefore, the isoclines have information about the amount of scatter, see Fig. 4 with $N = 1.2296$.

Last but not least, we demonstrated how the near-equilibrium behaviour of the stochastic model can be approximated with a diffusion formulation such that the conservation law for mass is respected. Although mass conservation is not frequently observed in population dynamic models, it is a cornerstone in DEB theory.

We have chosen this model for our analysis because it is the simplest involving key topics in population dynamics: mass conservation, satiating food uptake and stoichiometric constraints on secondary production. We here assumed that nutrient uptake is so efficient that there is hardly any free nutrient. By introducing explicit dynamics for the free nutrient in the environment, this system can be further reduced to e.g. a double Monod model, as studied in [23,24], or extended to a double Droop model [25], or a triple Monod model [26,27]. These variants do not include stoichiometric consequences of biomass with a varying chemical composition.

It is remarked that in the stochastic model producers and/or consumers will get extinct within a short time for N below the tangent bifurcation when the internal equilibrium gets deterministically unstable. Above the Hopf bifurcation we have a stable limit cycle with the property that for increasing N it will take values close to the boundaries $P = 0$ and $C_h = 0$. For extremely small P_ε values a cycle will break down with some probability each time when the system comes close to these boundaries. Thus, also for large N extinction is likely to occur within a short time. Within the range of N-values where a stable internal equilibrium is found the extinction time will rise to a large value. An analytical approximation of this extinction time was made for a system with a similar dynamics and compared with simulation results by [28].

Acknowledgement

This research has been supported by the Dutch National Research Programme 'Computational Life Sciences', Contract No. 635.100.013.

References

[1] D. DeAngelis, Dynamics of Nutrient Cycling and Food Webs, Chapman & Hall, London, 1992.
[2] S.A.L.M. Kooijman, T.R. Andersen, B.W. Kooi, Dynamic energy budget representations of stoichiometric constraints to population models, Ecology 85 (2004) 1230.
[3] S.A.L.M. Kooijman, Dynamic Energy and Mass Budgets in Biological Systems, Cambridge University, 2000.
[4] J. Grasman, O.A.v. Herwaarden, Asymptotic methods for the Fokker–Planck Equation and the Exit Problem in Applications, Springer, Berlin, 1999.
[5] C.W. Gardiner, Handbook of Stochastic Methods, Springer-Verlag, Berlin, 1983.
[6] J. Guckenheimer, P. Holmes, Nonlinear oscillations, dynamical systems and bifurcations of vector fields, Applied Mathematical Sciences, second ed., vol. 42, Springer-Verlag, New York, 1985.
[7] S. Wiggins, Introduction to Applied Nonlinear Dynamical Systems and Chaos, Texts in Applied Mathematics, vol. 2, Springer-Verlag, New York, 1990.
[8] Y.A. Kuznetsov, Elements of applied bifurcation theory, Applied Mathematical Sciences, second ed., vol. 112, Springer-Verlag, New York, 1998.
[9] E.J. Doedel, A.R. Champneys, T.F. Fairgrieve, Y.A. Kuznetsov, B. Sandstede, X. Wang, Auto 97: Continuation and bifurcation software for ordinary differential equations, Tech. rep., Concordia University, Montreal, Canada (1997).

[10] Y.A. Kuznetsov, V.V. Levitin, CONTENT: Integrated environment for the analysis of dynamical systems, Centrum voor Wiskunde en Informatica (CWI), Kruislaan 413, 1098 SJ Amsterdam, The Netherlands, first ed. (1997).
[11] T. Andersen, Pelagic Nutrient Cycles: Herbivores as Sources and Sinks, Springer-Verlag, Berlin, New York, 1997.
[12] S.A.L.M. Kooijman, T.A. Troost, Quantitative steps in the evolution of metabolic organisation as specified by the dynamic energy budget theory, Biol. Rev. 82 (2007) 1.
[13] R.W. Sterner, Daphnia growth on varying quality of *Scenedesmus*: mineral limitations of zooplankton, Ecology 74 (1993) 2351.
[14] T. Andersen, J.J. Elser, D.O. Hessen, Stoichiometry and population dynamics, Ecol. Lett. 7 (2004) 884.
[15] S.A.L.M. Kooijman, The synthesizing unit as model for the stoichiometric fusion and branching of metabolic fluxes, Biophys. Chem. 73 (1998) 179.
[16] E.B. Muller, R.M. Nisbet, S.A.L.M. Kooijman, J.J. Elser, E. McCauley, Stoichiometric food quality and herbivore dynamics, Ecol. Lett. 4 (2001) 519.
[17] D.T. Gillespie, A general method for numerically simulating the stochastic time evolution of coupled chemical reactions, J. Comput. Phys. 22 (1976) 403.
[18] J. Grasman, O.A.v. Herwaarden, T.J. Hagenaars, Resilience and persistence in the context of stochastic population models, in: T.A.C. Reydon, L. Hemerik (Eds.), Current Themes in Theoretical Biology, A Dutch Perspective, Springer, Dordrecht, 2005, p. 267.
[19] B.W. Kooi, Numerical bifurcation analysis of ecosystems in a spatially homogeneous environment, Acta Biotheor. 51 (3) (2003) 189.
[20] M.W. Hirsch, S. Smale, Differential Equations, Dynamical Systems, and Linear Algebra, Academic Press, New York, 1974.
[21] M.L. Rosenzweig, Paradox of enrichment: destabilization of exploitation ecosystems in ecological time, Science 171 (1971) 385.
[22] R.M. Nisbet, W.S.C. Gurney, Modelling fluctuating populations, John Wiley & Sons, Chichester, 1982.
[23] B.W. Kooi, S.A.L.M. Kooijman, Existence and stability of microbial prey–predator systems, J. Theor. Biol. 170 (1994) 75.
[24] B.W. Kooi, S.A.L.M. Kooijman, The transient behaviour of food chains in chemostats, J. Theor. Biol. 170 (1994) 87.
[25] S.A.L.M. Kooijman, B.W. Kooi, Catastrophic behaviour of myxamoebae, Nonlin. World 3 (1996) 77.
[26] B.W. Kooi, S.A.L.M. Kooijman, Many limiting behaviours in microbial food chains, in: O. Arino, M. Kimmel, D. Axelrod (Eds.), Mathematical Population Dynamics, Biological Systems, Wuerz Publ, Winnipeg, Canada, 1995, pp. 131.
[27] M.P. Boer, B.W. Kooi, S.A.L.M. Kooijman, Homoclinic and heteroclinic orbits in a tri-trophic food chain, J. Math. Biol. 39 (1999) 19.
[28] J. Grasman, M.d. Gee, O.A.v. Herwaarden, Breakdown time of a chemostat exposed to stochastic noise, J. Eng. Math. 53 (2005) 291.