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"Existence and Stability of Microbial Prey-Predator Systems"

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Existence and Stability of Microbial Prey–Predator Systems

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A model for food uptake, energy conversion and allocation is proposed for individuals that propagate by fission. When simple assumptions for the environment and interactions between substrate, prey and predator in a chemostat are made, the conservation laws for energy and biomass determine a structured population model. This model is compared with lumped models from the literature, such as the "Double Monod model". Individual-based models consistent with these lumped models, are derived and compared. Expressions for the parameters of the lumped model are found as functions of parameters in the model for the individuals making up the population. To reduce the number of parameters body-size scaling relations are used. The existence and stability of equilibria under chemostat conditions are studied. The dynamics of the substrate, bacterial prey and protozoan predator depend substantially on the underlying model for the individuals.

1. Introduction

In this paper the consequences of a simple model for the input–output behaviour of individuals interacting in prey–predator systems under chemostat conditions are studied. Fresh medium, in which all components for growth of the bacterial prey except carbohydrates are present in abundance, is pumped through the chemostat with complete mixing. The bacteria are preyed upon by protozoa. There is no interaction between conspecific individuals other than that they feed on the same resource. In addition to predation no losses of individuals other than the wash-out are considered. We focus on individuals which propagate through fission into two equal parts, as is appropriate, for example, for most bacteria, some unicellular eukaryotes, planarians and some oligochaetes. The model for the individuals is the "dynamic energy budget" (DEB) model, that has been proposed in Kooijman (1993) and successfully applied to microbes in Kooijman *et al.* (1991). It is described in Section 2.

The primary aim is to test its consequences against current models such as the "Double Monod" (DM) model for existence and stability of microbial prey–predator systems under chemostat conditions. The usage of the DM model in chemostat situations is described in Nisbet *et al.* (1983), Sambanis *et al.* (1987) and Tsangaropoulou & Pavlou (1990). Individual-based models, consistent with different variants of the DM model, are derived in Section 3. The used theory of structural population dynamics is developed in Metz & Diekmann (1986). Models for such populations are also called segregated models: see Fredrickson (1991). Parameters of the obtained lumped population models, such as the growth and yield, are expressed as functions of parameters of the individuals making up the population. One of the basic assumptions made in the DM model is that the yield is constant. An individual based model makes it possible to derive this assumption from assumptions with respect to the behaviour of the individuals making up the population.

We study a food chain of bacteria and ciliates in the chemostat described in Cunningham & Nisbet (1983) and Nisbet *et al.* (1983). Some assumptions—fixed length at division, division into two equal daughters—made for the individual level are more realistic

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for the bacteria than for the ciliates. The oral apparatus of ciliates is non-functional during replication, and therefore large individuals lose the ability to feed some time before they divide, and the newborn individuals do not regain this ability until some time after they have been formed by fission (see Fredrickson, 1991). However, our aim is to model also longer food chains in the reactor (see Kooi & Kooijman, 1993). Then, in order to keep the number of parameters limited, one cannot handle mathematical models that are too species-specific.

The region of stability of the food chain in the chemostat for the two control parameters – the dilution rate and the substrate density of the inflowing medium – depends largely on the underlying mathematical model for the growth of the individuals. We obtain the result reported in Nisbet *et al.* (1983) that the introduction of maintenance has a stabilizing effect especially for low dilution rates. A new result is that when energy reserves are modelled, wash-out occurs at much lower dilution rates and that the region of stability is smaller.

To reduce complexity, we assume that surface area is proportional to the volume of the individuals. This is only realistic for filaments, therefore this model is called the DEBf (see Section 4). It is shown that this assumption has little effect on the dynamic behaviour of chemostats.

The DEBf model is equivalent to a straightforward extension of the Monod model with maintenance (proposed by Pirt, 1965) and energy reserves (proposed by Droop, 1973).

This led us to apply the DEBf model to fit time-course data published by Dent *et al.* (1976). They were unable to obtain good quantitative agreement between theory (Monod model) and experimental results. In the companion paper (Kooi & Kooijman, 1994) we show that the DEBf model predicts the data very well and that both maintenance and energy reserves are necessary to explain a number of phenomena observed and which could not be understood using the Monod model.

2. Formulation of the Problem

In this section we start with the DEB model for both prey and predator individuals. Based on this model, the models for the populations and for the whole chemostat system are derived.

THE DEB MODEL FOR INDIVIDUALS

In the DEB model energy reserve is a second state variable in addition to size. Such a buffer imposes some kind of inertia with respect to the response to changing food conditions. It is motivated by the observation that organisms undergoing a sharp change in food density adapt only gradually to a new growth rate. Metabolic maintenance costs at the individual level are also introduced. The model is mechanistic and in various papers it is shown to be a useful model for the description of growth of individuals from all over the animal kingdom, including egg development and mammalian embryonic growth (see Kooijman, 1986*a*, *b*, *c*). For a description of the model see Kooijman (1993).

The individual growth model is described by a system of two ordinary differential equations for the volumetric length l_i being the cubic root of the volume of the individual and the energy reserves density e_i both as functions of the time τ

$$\frac{\mathrm{d}}{\mathrm{d}\tau}e_i = v_i\frac{f_{i-1,i}-e_i}{l_i} \quad \text{with} \quad f_{i-1,i}=\frac{x_{i-1}}{k_{i-1,i}+x_{i-1}} \tag{1}$$

$$\frac{\mathrm{d}}{\mathrm{d}\tau}l_i = \frac{v_i}{3}\frac{e_i - l_i/l_{m_i}}{e_i+g_i} \quad \text{with} \quad l_{m_i}=\frac{v_i}{m_i g_i}, \tag{2}$$

with $i = 1, 2$ for the bacterial prey and protozoan predator, respectively. The first equation models that there is a force driving to homeostasis. The second that energy from the reserves are used for growth and maintenance. For the biological meaning of the parameters refer to Kooijman (1993) and Table 1. The quantity x_{i-1} is the density of the food. The functional response $f_{i-1,i}$ is Holling type II.

We assume that the individual propagates by binary fission into two equal parts. The length at division is denoted by l_{d_i}. So, the introduction of two equal new individuals occurs at length $l_{b_i} = 2^{-1/3}l_{d_i}$ with the same energy density as the mother individual. The length l_{m_i} is the maximum length an individual might reach when it would not divide. When $e_i < l_i/l_{m_i}$ eqn (2) shows that the individual shrinks, but we assume in this study that $l_{d_i}/l_{m_i} \leqslant e_i \leqslant 1$.

THE MODEL FOR THE PREY AND PREDATOR SYSTEM

Let $n_i(\tau, e_i, l_i)$ denote the density of individuals having energy density e_i and length l_i at time τ, so that

$$\int_{e_a}^{e_b}\int_{l_a}^{l_b} n_i(\tau, e_i, l_i)\,\mathrm{d}l_i\,\mathrm{d}e_i$$

is the number of individuals per volume of reactor with an energy density between $e_i = e_a$ and $e_i = e_b$ and a length between $l_i = l_a$ and $l_i = l_b$ at time τ. Suppose that we take individuals out of the population at a constant probability rate $p_{i,i+1}$ per individual per unit of time. This term takes predation as well as dilution into account.

2.

TABLE 1

Parameters and state variables: t = *time*, l_i = *cubic root of the volume of the individual*, l_r = *cubic root of the volume of the reactor*, e = *energy*

Parameter	Dimension DEB model	Dimension DEBf model	Interpretation
τ	t	t	Time
l_i	l_i	l_i	Length of individual
e_i	—	—	Ratio of energy reserves and its maximum value
$k_{i-1,i}$	$\mathrm{l}_i^3 \cdot \mathrm{l}_r^{-3}$	$\mathrm{l}_i^3 \cdot \mathrm{l}_r^{-3}$	Saturation constant
$I_{m_{i-1,i}}$	$\mathrm{l}_i \cdot \mathrm{t}^{-1}$	t^{-1}	Maximum food uptake rate
v_i, ν_i	$\mathrm{l}_i \cdot \mathrm{t}^{-1}$	t^{-1}	Energy conductance in DEB and DEBf model ∝ assimilation rate
g_i	—	—	Energy investment ratio, ∝ costs for growth
m_i	t^{-1}	t^{-1}	Maintenance rate coefficient
l_{d_i}	l_i	l_i	Length at division
$l_{b_i} = 2^{-1/3} l_{d_i}$	l_i	l_i	Length after division
x_i	$\mathrm{l}_i^3 \cdot \mathrm{l}_r^{-3}$	$\mathrm{l}_i^3 \cdot \mathrm{l}_r^{-3}$	Biovolume
$f_{i-1,i}$	—	—	Functional response
$p_{i,i+1}$	t^{-1}	t^{-1}	Efflux of individuals
n_i	$\mathrm{l}_i^2 \cdot \mathrm{l}_r^{-3} \cdot \mathrm{e}^{-1}$	$\mathrm{l}_i^2 \cdot \mathrm{l}_r^{-3} \cdot \mathrm{e}^{-1}$	Density of individuals
x_r	$\mathrm{l}_i^3 \cdot \mathrm{l}_r^{-3}$	$\mathrm{l}_i^3 \cdot \mathrm{l}_r^{-3}$	Substrate concentration in reservoir
D	t^{-1}	t^{-1}	Dilution rate
x_0	$\mathrm{l}_i^3 \cdot \mathrm{l}_r^{-3}$	$\mathrm{l}_i^3 \cdot \mathrm{l}_r^{-3}$	Substrate density
μ	t^{-1}	t^{-1}	Overall population growth rate
y	—	—	Yield

Under the regime described above, we have:

$$\frac{\partial}{\partial \tau} n_i(\tau, e_i, l_i) = -\frac{\partial}{\partial l_i}\left(n_i(\tau, e_i, l_i)\frac{\mathrm{d}}{\mathrm{d}\tau} l_i\right) - \frac{\partial}{\partial e_i}\left(n_i(\tau, e_i, l_i)\frac{\mathrm{d}}{\mathrm{d}\tau} e_i\right) - p_{i,i+1} n_i(\tau, e_i, l_i), \tag{3}$$

where $(\mathrm{d}/\mathrm{d}\tau)e_i$ and $(\mathrm{d}/\mathrm{d}\tau)l_i$ are given in eqn (1) and (2), respectively. The boundary condition for the hyperbolic partial differential eqn (3) reads

$$n_i(\tau, e_i, l_{b_i})\left.\frac{\mathrm{d}l_i}{\mathrm{d}\tau}\right|_{l_i = l_{b_i}} = 2n_i(\tau, e_i, l_{d_i})\left.\frac{\mathrm{d}l_i}{\mathrm{d}\tau}\right|_{l_i = l_{d_i}}. \tag{4}$$

Substitution of eqn (2) yields

$$n_i(\tau, e_i, l_{b_i}) = 2n_i(\tau, e_i, l_{d_i})\frac{e_i - l_{d_i}/l_{m_i}}{e_i - l_{b_i}/l_{m_i}}. \tag{5}$$

Hence, the fission is tied to the growth process. This formulation deviates from the ones used, for example, by Sinko & Streifer (1967) and Metz & Diekman (1986) who treat both processes as independent ones. Note that we do not need to prescribe conditions at the other two boundaries of the region in the *e*, *l* plane because the boundaries are moving boundaries. The positions of these boundaries are part of the solution of the governing equations.

THE CHEMOSTAT SYSTEM

The individuals of the prey and the predator in the chemostat follow the DEB model with respect to their change in energy density and length, but the parameters generally differ. We sandwich each population between an influx of food and an efflux of individuals.

Suppose that the substrate density in the inflowing medium is constant at value x_r. Then the supply rate of substrate flowing into the chemostat is Dx_r where the rate of dilution D is the quotient of the rate of flow of fresh medium and the volume of the reactor. We assume complete mixing, so that the environment is homogeneous.

In what follows some statistics will be of particular interest: the total number of individuals

$$\mathcal{N}_i(\tau) = \int_{l_i = l_{b_i}}^{l_{d_i}} \int_{e_i = l_{d_i}/l_{m_i}}^{1} n_i(\tau, e_i, l_i)\,\mathrm{d}e_i\,\mathrm{d}l_i, \tag{6}$$

the mean surface area

$$\mathcal{E} l_i^2 \equiv \mathcal{N}_i(\tau)^{-1} \int_{l_i = l_{b_i}}^{l_{d_i}} \int_{e_i = l_{d_i}/l_{m_i}}^{1} l_i^2 n_i(\tau, e_i, l_i)\,\mathrm{d}e_i\,\mathrm{d}l_i, \tag{7}$$

and the mean biovolume

$$\mathcal{E} l_i^3 \equiv \mathcal{N}_i(\tau)^{-1} \int_{l_i = l_{b_i}}^{l_{d_i}} \int_{e_i = l_{d_i}/l_{m_i}}^{1} l_i^3 n_i(\tau, e_i, l_i)\,\mathrm{d}e_i\,\mathrm{d}l_i. \tag{8}$$

Using these notions the coupling between the substrate and the prey is given by

$$(p_{0,1} - D)x_0 = I_{m_{0,1}} f_{0,1} \mathcal{N}_1(\tau)\mathcal{E} l_1^2, \tag{9}$$

3.

where $p_{0,1}$ is the rate the substrate leaves the reactor because of consumption by bacteria and wash-out, and

$$f_{0,1} = \frac{x_0}{k_{0,1} + x_0}. \qquad (10)$$

For the inter-level coupling we assume that the prey uptake rate of the predator ($i = 2$) equals the biovolume drain rate of the prey ($i = 1$) and we take into account the losses due to medium throughput. Thus there is only a coupling via biovolumes conversion and not via the energy storages. For the coupling between the prey and the predator we have

$$(p_{1,2} - D)\mathcal{N}_1(\tau)\mathcal{E}l_1^3 = I_{m_{1,2}} f_{1,2} \mathcal{N}_2(\tau)\mathcal{E}l_2^2, \qquad (11)$$

where $p_{1,2}$ is the rate the bacteria leave the reactor because of consumption by ciliates and wash-out, and

$$f_{1,2} = \frac{\mathcal{N}_1(\tau)\mathcal{E}l_1^3}{k_{1,2} + \mathcal{N}_1(\tau)\mathcal{E}l_1^3}. \qquad (12)$$

Because we do not consider predation of the top predator we have

$$p_{2,3} = D, \qquad (13)$$

that is, the ciliate leave the reactor only because of wash-out. Notice that the functional response, the saturation constant and the predation have double sub-indexes to emphasize that these quantities depend on both substrate-prey relations (0, 1) and prey predator relations (1, 2), respectively. Finally the equation of continuity for the substrate reads

$$\frac{d}{d\tau}x_0 = Dx_r - p_{0,1}x_0. \qquad (14)$$

In summary the mathematical model consists of a system of one ordinary differential equation (ODE) (14) and a set of two first-order hyperbolic partial differential equations (PDE) (3) with boundary conditions (5), coupled by conditions (9) and (11). Together with the initial condition for the population densities $n_i(0, e_i, l_i)$, $i = 1,2$, which we assume to be sufficiently smooth, and the substrate density $x_0(0)$, this set of equations fully determines the dynamics of the substrate and the populations. The input parameters for the chemostat are v_i, g_i, $k_{i-1,i}$, $I_{m_{i-1,i}}$, m_i and l_{d_i}, for $i = 1, 2$. The concentration of the substrate x_r in the inflowing medium and the dilution rate D are assumed to be under experimental control.

FROM FULL STRUCTURE TO NO STRUCTURE

One can wonder to what extent we have to keep track of the dynamic changes in the population when the interest is only in its global behaviour. First, we try to apply a method proposed by MacDonald (1978) and by Murphy (1983) called the "linear chain trick" (see also Metz & Dieckmann, 1989; Cushing, 1989). In that approach the equations for one population derived in the previous section become equivalent to a set of ODEs. With the statistics defined in eqns (6), (7) and (8) we obtain by integrating by parts:

$$\frac{d}{d\tau}\mathcal{N}_i = \int_{e_i} n_i(\tau, e_i, l_{d_i}) \left.\frac{dl_i}{d\tau}\right|_{l_{d_i}} de_i - p_{i,i+1}\mathcal{N}_i \qquad (15)$$

$$\begin{aligned}\frac{d}{d\tau}\mathcal{N}_i\mathcal{E}l_i^2 = 2\int_{l_i}\int_{e_i} l_i n_i(\tau, e_i, l_i)\frac{dl_i}{d\tau}\, de_i\, dl_i \\ - p_{i,i+1}\mathcal{N}_i\mathcal{E}l_i^2 - (1 - 2^{-1/3})l_{d_i}^2 \\ \times \int_{e_i} n(\tau, e_i, l_{d_i})\left.\frac{dl_i}{d\tau}\right|_{l_{d_i}} de_i \end{aligned} \qquad (16)$$

$$\begin{aligned}\frac{d}{d\tau}\mathcal{N}_i\mathcal{E}l_i^3 = 3\int_{l_i}\int_{e_i} l_i^2 n_i(\tau, e_i, l_i) \\ \times \frac{dl_i}{d\tau}\, de_i\, dl_i - p_{i,i+1}\mathcal{N}_i\mathcal{E}l_i^3.\end{aligned} \qquad (17)$$

These equations show that in our case, because of the form of the boundary condition (5), we do not end up with a set of ODEs for the substrate concentration x_0 and the statistics for the distribution of the population $n_i(\tau, e_i, l_i)$, $i = 1, 2$. Therefore we try to simplify the system in another way by stripping the population from its internal structure. We do this in two steps.

We assume that the energy density for all individuals will approach the value $e = f$, also when f is still a function of time τ. Then, eqn (2) reduces to

$$\frac{d}{d\tau}l_i = \frac{v_i}{3}\frac{f_{i-1,i} - l_i/l_{m_i}}{f_{i-1,i} + g_i}, \qquad (18)$$

Substitution of this equation in eqn (17) where n_i is a function of time τ and size l_i only, yields

$$\begin{aligned}\frac{d}{d\tau}\mathcal{N}_i\mathcal{E}l_i^3 = \bigg(\frac{v_i f_{i-1,i}}{f_{i-1,i} + g_i}\frac{\mathcal{E}l_i^2}{\mathcal{E}l_i^3} \\ - \frac{g_i m_i}{f_{i-1,i} + g_i} - p_{i,i+1}\bigg)\mathcal{N}_i\mathcal{E}l_i^3.\end{aligned} \qquad (19)$$

Now we define the overall population growth rate $\mu_{i-1,i}$ with

$$\mu_{i-1,i} = \frac{v_i f_{i-1,i}}{f_{i-1,i} + g_i}\frac{\mathcal{E}l_i^2}{\mathcal{E}l_i^3} - \frac{g_i m_i}{f_{i-1,i} + g_i}. \qquad (20)$$

This result can be used to eliminate the $\mathcal{E}l_{i-1}^2$ term in the interlevel conditions (9) and (11) and we obtain

$$\begin{aligned}p_{i-1,i} - D = I_{m_{i-1,i}}\frac{(f_{i-1,i} + g_i)\mu_{i-1,i} + g_i m_i}{v_i} \\ \times \frac{\mathcal{N}_i\mathcal{E}l_i^3}{\mathcal{N}_{i-1}\mathcal{E}l_{i-1}^3}.\end{aligned} \qquad (21)$$

4.

Now we are able to define the variable x_i used for the food density in the expression for the functional response $f_{i-1,i}$ in eqn (1) precisely being the biovolumes $x_i = \mathcal{N}_i \delta l_i^3$ for $i = 1, 2$. Then we end up with a set of three coupled differential equations for the substrate density x_0 and the total biovolume of the prey x_1 and predator x_2. To compare these expressions with those mentioned in the literature we define the conversion coefficient $y_{i-1,i}$ concerning conversion of biomass x_{i-1} into biomass x_i as

$$y_{i-1,i} = \frac{\mu_{i-1,i} x_i}{(p_{i-1,i} - D)x_{i-1}}, \tag{22}$$

where $\mu_{i-1,i}$ is given by eqn (20) and $p_{i-1,i}$ by (21). The use of these equations gives the following expression for the yield $y_{i-1,i}$

$$y_{i-1,i} = \frac{\mu_{i-1,i} v_i}{l_{m_{i-1}}((g_i + f_{i-1,i})\mu_{i-1,i} + g_i m_i)}. \tag{23}$$

Equations (14) and (19) become, for $i = 0$,

$$\frac{\mathrm{d}}{\mathrm{d}\tau} x_0 = D(x_r - x_0) - \frac{\mu_{0,1}}{y_{0,1}} x_1, \tag{24}$$

for $i = 1$

$$\frac{\mathrm{d}}{\mathrm{d}\tau} x_1 = (\mu_{0,1} - D)x_1 - \frac{\mu_{1,2}}{y_{1,2}} x_2, \tag{25}$$

and for $i = 2$

$$\frac{\mathrm{d}}{\mathrm{d}\tau} x_2 = (\mu_{1,2} - D)x_2. \tag{26}$$

The initial conditions $x_0(0)$, $x_1(0)$ and $x_2(0)$ complete the formulation of the problem.

However, the growth rate $\mu_{i-1,i}$ [eqn (20)] depends on the length distribution of the individuals. To facilitate the transition form the individual level to the population level we set the energy density at the value it would have at prolonged constant food densities f, such that $l_d/l_m < e = f \leqslant 1$. In that case the growth is of the Von Bertalanffy type and the PDE (3), where n_i is a function of time τ and size l_i, reduces to

$$\frac{\partial}{\partial\tau} n_i(\tau, l_i) = -\frac{\partial}{\partial l_i}\left(n_i(\tau, l_i)\frac{\mathrm{d}}{\mathrm{d}\tau} l_i\right) - p_{i,i+1} n_i(\tau, l_i), \tag{27}$$

while the boundary condition (5) becomes

$$n_i(\tau, l_{b_i}) = 2n_i(\tau, l_{d_i})\frac{f_{i-1,i} - l_{d_i}/l_{m_i}}{f_{i-1,i} - l_{b_i}/l_{m_i}}. \tag{28}$$

The method of separation of variables yields the solution

$$n_i = n_{i_0} \exp\{(\mu_{i-1,i} - p_{i,i+1})\tau\} \times \left(\frac{v_i}{3}\frac{f_{i-1,i} - l_i/l_{m_i}}{f_{i-1,i} + g_i}\right)^{\frac{\ln 2}{\ln \frac{f_{i-1,i} - l_{b_i}/l_{m_i}}{f_{i-1,i} - l_{d_i}/l_{m_i}}}}, \tag{29}$$

where $\mu_{i-1,i}$ is the overall population growth rate, equivalent to the quantity defined in eqn (20) (see also Kooijman *et al.*, 1991).

$$\mu_{i-1,i} = \frac{v_i/l_{m_i}}{3(f_{i-1,i} + g_i)} \frac{\ln 2}{\ln \frac{f_{i-1,i} - l_{b_i}/l_{m_i}}{f_{i-1,i} - l_{d_i}/l_{m_i}}}. \tag{30}$$

The constant n_{i_0} is given by the initial length distribution for $\tau = 0$. Observe that the last factor of eqn (29) shows that the length distribution depends on the food densities f.

In what follows we investigate the situation in which the states of substrate, prey and predator are relatively close to the steady state. We assume that the energy density and length distribution are adjusted instantaneously to changing food densities. Then eqn (30) remains valid also for varying food densities $f(\tau)$.

Notice that this method does not yield the solution of the arbitrary initial value problem for the complete DEB model. To solve initial value problems with variable food supply numerically one can use, for example, the "Escalator boxcar train" method developed in de Roos (1988).

3. Comparison with DM Models

The equations derived in the preceding section resemble those of the DM model given for example in Nisbet *et al.* (1983). The classical and still very popular Monod model (Monod, 1942) deals with the population level but it makes implicit assumptions for the individual level, which we make explicit first. The procedure followed in the preceding section is now repeated with assumptions compatible with the DM model. Hence we start again at the individual level where propagation is by fission. Thereafter the population dynamics is derived and finally the dynamics of the chemostat.

THE DM MODEL

In the DM model the growth of the individuals is given by

$$\frac{\mathrm{d}}{\mathrm{d}\tau} l_i = \frac{v_i/g f_{i-1,i} l_i}{3}. \tag{31}$$

The growth rate's being proportional to the length depends on the density of the food f. In this case v_i/g_i has to be regarded as one compound parameter, being the maximum growth rate of the individual on the basis of volume. Under this regime, the population level is described by the PDE

$$\frac{\partial}{\partial \tau} n_i(\tau, l_i) = -\frac{\partial}{\partial l_i}\left(n_i(\tau, l_i)\,\frac{v_i/g_i f_{i-1,i}}{3}\, l_i\right) - p_{i,i+1} n_i(\tau, l_i). \quad (32)$$

The boundary condition for the PDE becomes

$$n_i(\tau, l_{b_i}) = 2^{4/3} n_i(\tau, l_{d_i}) \text{ where } \quad 2^{1/3} l_{b_i} = l_{d_i}. \quad (33)$$

We use the equivalent of eqn (17) and obtain

$$\frac{\mathrm{d}}{\mathrm{d}\tau} x_i = (v_i/g_i f_{i-1,i} - p_{i,i+1}) x_i. \quad (34)$$

We see that for the DM model the growth rate of each individual $v_i/g_i f_{i-1,i}$ equals the overall population growth rate $\mu_{i-1,i}$. Because the growth is proportional to the volume of the individuals and because at fission there is continuity of biovolume, it makes no difference whether the population consists initially of one large individual or many small ones. This shows that for the DM model the unstructured and structured models for the population level are the same. The governing equations are equivalent with the equations (24), (25) and (26) with the following expression for $y_{i-1,i}$

$$y_{i-1,i} = \frac{\mu_{i-1,i}}{I_{m_{i-1,i}} f_{i-1,i}}. \quad (35)$$

Using Monod's equation

$$\mu_{i-1,i} = \mu_{m_{i-1,i}} f_{i-1,i}, \quad (36)$$

we obtain

$$y_{i-1,i} = \frac{\mu_{m_{i-1,i}}}{I_{m_{i-1,i}}}, \quad (37)$$

where $\mu_{m_{i-1,i}}$ is the maximum growth rate obtained when $f \to 1$. In this case the conversion coefficients $y_{i-1,i}$ depend only on the parameters $I_{m_{i-1,i}}$ and $\mu_{m_{i-1,i}}$ and it will be denoted as $y_{m_{i-1,i}}$. Thus the well-known assumption of a constant yield coefficient in the DM model can be inferred from assumptions concerning the individual level.

DM MODELS WITH COSTS FOR MAINTENANCE

In this subsection extensions to the DM model to take maintenance energy into account are described. We deal with two equivalent formulations, the endogenous metabolism and the maintenance energy requirement.

Herbert (1958) accounted for endogenous metabolism in growing bacteria by a modification of the growth rate law. Then the Monod equation for growth μ is replaced by

$$\mu_{i-1,i} = \mu_{m_{i-1,i}} f_{i-1,i} - m_i, \quad (38)$$

where m_i is the maintenance rate coefficient. We obtain for the yield $y_{i-1,i}$

$$\frac{1}{y_{i-1,i}} = \frac{m_i}{y_{m_{i-1,i}} \mu_{i-1,i}} + \frac{1}{y_{m_{i-1,i}}}. \quad (39)$$

The DM model with costs for maintenance is termed the Marr–Pirt model.

For the sake of completeness we mention another model proposed by Pirt (1965) in which the overall rate of food utilization is set equal to the rate of food utilization for maintenance plus the rate of food utilization for growth. Then the yield is no longer a constant. It is given by

$$\frac{1}{y_{i-1,i}} = \frac{M_{P_i}}{\mu_{P_{i-1,i}}} + \frac{1}{y_{G_{i-1,i}}}, \quad (40)$$

where the subscript P denotes Pirt's model. The constants M_{P_i} are called the maintenance coefficient and the constants $y_{G_{i-1,i}}$ are termed "true growth yield". These expressions have to be substituted in eqns (24) and (25).

It is easy to show that both approaches lead to the same mathematical equations if we assume the following relationships between the parameters of the different models:

$$M_{P_i} = \frac{m_i}{y_{m_{i-1,i}}}, \quad \mu_{P_{i-1,i}} = \mu_{i-1,i} - m_i,$$
$$y_{G_{i-1,i}} = y_{m_{i-1,i}}. \quad (41)$$

DM MODELS WITH INTERNAL MASS STORAGE

Droop (1973) extended the DM model into another direction, namely, the introduction of reserves via mass storage. In a simplified Droop model for phytoplankton it is assumed that growth is not controlled by the concentration of limiting nutrient in the reactor but rather by the concentration of the nutrient q present within the individuals themselves. For the prey and predator system this leads to additional differential equations for both levels,

$$\frac{\mathrm{d}}{\mathrm{d}\tau} q_i = I_{m_{i-1,i}} f_{i-1,i} - \mu_{i-1,i} q_i, \quad (42)$$

for $i = 1, 2$, where q_i is the so-called quota of limiting nutrient.

The growth function is given by

$$\mu_{i-1,i} = \frac{\mu'_{m_i}(q_i - k_{q_{i-1,i}})}{k_{q_{i-1,i}} + (q_i - k_{q_{i-1,i}})}, \quad (43)$$

where μ'_{m_i} is the maximum specific growth rate at infinite internal food concentration and $k_{q_i,i-1,i}$ the value of q for zero μ.

This completes the formulation of the DM model with two variants of Marr–Pirt and Droop. In the next subsection these models are compared with a special variant of the DEB model.

4. The DEBf Model

In this section we introduce energy reserves and metabolic maintenance costs at the individual level as in the DEB model. We make an additional assumption that the surface area is proportional to the volume of the individual. In filaments, which, unlike isomorphs grow in length, surface area is proportional to volume. Thus this model is the DEB model for filaments and will be referred to as the DEBf model (see Kooijman *et al.*, 1991). Observe that by definition the length (l) is still the cubic root of the volume of the individual rather than its real physical length.

The equations for the individual energy storage and growth now become

$$\frac{\mathrm{d}}{\mathrm{d}\tau}e_i = v_i(f_{i-1,i} - e_i) \quad \text{with} \quad f_{i-1,i} = \frac{x_{i-1}}{K_{i-1,i} + x_{i-1}} \tag{44}$$

$$\frac{\mathrm{d}}{\mathrm{d}\tau}l_i = \frac{v_ie_i - g_im_i}{3(e_i + g_i)}l_i, \tag{45}$$

where v_i is the specific energy conductance which relates to the energy conductance v_i in the DEB model. Later we will make this relationship explicit.

As in the DEB model, for the population level we have the PDE (3) where $(\mathrm{d}/\mathrm{d}\tau)e_i$ and $(\mathrm{d}/\mathrm{d}\tau)l_i$ are given in (44) and (45), respectively. The boundary condition for the PDE in this case is expressed by eqn (33) as in the case of the DM model. For the coupling between substrate, prey and predator we have the same expressions as those of the DEB model. Equation (17) for the DEBf model becomes

$$\frac{\mathrm{d}}{\mathrm{d}\tau}x_i = \int_{l_i}\int_{e_i} l_i^3 n_i(\tau, e_i, l_i)\frac{v_ie_i - g_im_i}{(e_i + g_i)}\,\mathrm{d}e_i\,\mathrm{d}l_i - p_{i,i+1}x_i. \tag{46}$$

When $f(\tau)$ is a function of time the value for $e(\tau)$ for each individual converges exponentially to same time-path, so that $e(\tau)$ can be interpreted as the reserve density of a randomly chosen individual at time τ [see eqn (44)]. (Mathematically this means that the support of the density $n(e, l)$ reduces from two to one dimension.) Then, eqns (24), (25), (26) and (44) are obtained together with (35) and

$$\mu_{i-1,i} = \frac{v_ie_i - g_im_i}{e_i + g_i}. \tag{47}$$

This model becomes the Droop model when there are no costs for maintenance. When $m = 0$ the DEBf model is equivalent to the DM model with internal reserves given by eqns (24), (25), (26) and (42), where the growth rate is given by eqn (43). With

$$q_i - k_{q_i,i-1,i} = \frac{I_{m_i,i-1,i}}{v_i}e_i, \tag{48}$$

it is easy to derive the relationships

$$\mu'_{m_i} = v_i \quad \text{and} \quad k_{q_i,i-1,i} = \frac{g_iI_{m_i,i-1,i}}{v_i}. \tag{49}$$

The growth rate becomes with $m = 0$ in eqn (47)

$$\mu_{i-1,i} = \frac{v_ie_i}{e_i + g_i}, \tag{50}$$

and this shows that the DEBf model becomes the Droop model when there are no maintenance costs, for substitution of eqns (49) and (48) in eqn (50) yields eqn (43).

For constant food density $f_{i-1,i}$ the method of separation of variables gives the following solution for the PDE (3) with boundary condition (33)

$$n_i = n_{i_0}\exp\left\{\left(v_i + \frac{v_if_{i-1,i} - g_im_i}{f_{i-1,i} + g_i} - p_{i,i+1}\right)\tau\right\}$$
$$\times\, l_i^{-4}(g_i + e_i)^{-\frac{g_i(v_i + m_i)}{v_i(f_{i-1,i} + g_i)}}, \tag{51}$$

where n_{i_0} is given by the specific initial volume–energy distribution for $\tau = 0$. The overall population growth rate is now

$$\mu_{i-1,i} = \frac{v_if_{i-1,i} - g_im_i}{f_{i-1,i} + g_i}. \tag{52}$$

This is clarified as follows. The length of the range of interest for the energy density $e_i(\tau)$ goes to zero proportional with $e^{-v_i\tau}$ [see eqn (44)]. On the other hand, in the limit $\tau \to \infty$ with $\mu_{i-1,i} = p_{i,i+1}$, the population density $n_i(\tau, e_i, l_i) \to \infty$ as $\mathrm{e}^{v_i\tau}$. This suggests that the integral $\int_{l_i}\int_{e_i} n_i(\tau, e_i, l_i)\,\mathrm{d}e_i\,\mathrm{d}l_i$ remains finite for $\tau \to \infty$ as expected.

Equation (51) suggests that for $\tau \to \infty$ the length distribution of the population density becomes proportion to l_i^{-4} which is independent of the food density, in contrast with the DEB model: see eqn (29). However, with exponential growth, as described by eqn (45), it is well known (see Metz & Diekmann, 1986) that there is no convergence of the length

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distribution (see also Kooi & Kooijman, 1993). In more realistic biological models, for instance in which propagation is through fission into two unequal daughters, there is convergence to a "stable length distribution" and in those cases l_i^4 is a good approximation: see Kooijman *et al.* (1991). There is no convergence to the energy distribution as suggested by the last factor of eqn (51) either. This is immediately clear from eqn (44).

This completes the description of the DEBf model. In what follows we show that it can be interpreted as a straightforward extension of the DM models.

When we assume that the energy density is adjusted instantaneously to changing food densities, so that $e(\tau) = f(\tau)$ for all individuals, we obtain equations for the chemostat which resemble those of the DM model. In this situation, as in the DM model, the governing equations are equivalent with (24), (25), (26) and (35) with the Monod equation for $\mu_{i-1,i}$ replaced by eqn (52).

When there are no energy reserves, i.e. when $g \to \infty$, $v \to \infty$ so that $v/g \to \mu_{m_i,i-1,i}$, $e \to f$ and $m \neq 0$ the DEBf model is equivalent with the Marr Pirt model. There is a term representing the loss of biomass for maintenance eqn (38), and the yield is not a constant but is given by eqn (35). When there are also no maintenance costs, i.e. when $m = 0$, the DM and DEBf models are the same with $v/g \to \mu_{m_i,i-1,i}$.

5. Results

To illustrate the dynamic behaviour of the chemostat we present several "operating diagrams". In these bifurcation diagrams the dynamics of the system are shown as a function of the control parameters, the rate of dilution D and concentration of substrate x_r. The results in the operating diagrams are based upon local stability analysis for the approximating lumped-parameter population dynamic models. We used standard techniques which are not described here. In these diagrams the region with total washout is indicated with a "O" and with washout of the top predator with a "I"; see for example Fig. 1. In the first region the biomasses x_1 and x_2 for steady state are zero while $x_0 = x_r$. In the second region only x_2 is zero. In the latter case only bacteria are present in the chemostat. For this case the equilibrium is stable. In region II there is stable co-existence of both species and in region III unstable co-existence, limit cycles. The line between these regions marks a non-catastrophic or super-critical Hopf bifurcation.

A list of the chemostat parameters for the different models is presented in Table 2. The selection of a comparable set of the parameters for the DEB models is not unique. The parameters are chosen so that all parameters are the same in the limiting case when all models degenerate to the Monod model.

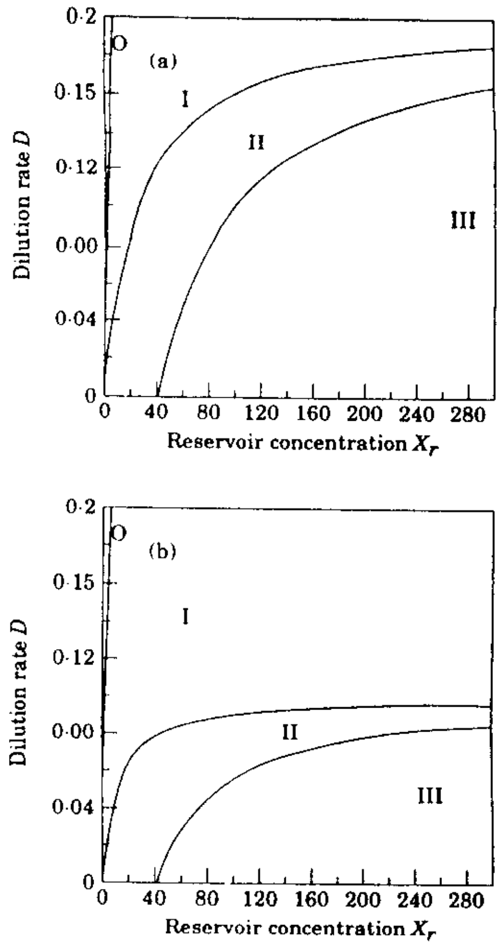

FIG. 1. Operating diagrams for the DEB model with no costs for routine metabolism, $\rho_1 = 0$ and $\rho_2 = 0$. (a) Diagram for the DM model. (b) Diagram for the DEBf model both with no costs for routine metabolism, $\rho_1 = 0$ and $\rho_2 = 0$, and with energy reserves, $g_1 = 80$ and $g_2 = 1$. The values assigned to the physiological parameters are listed in Table 2. The regions shown are (O) total wash-out, (I) wash-out of top predator, (II) stable co-existence of both species and (III) unstable co-existence.

One of the important parameters is the maximum possible growth rate $\mu_{m_i,i-1,i}$. This is the growth rate when abundant food is available, i.e. $f \to 1$ and when there are no maintenance costs $m = 0$. For the DM model eqn (36) shows that the nomenclature is adequate. When there are energy reserves but no maintenance costs, i.e. when $m = 0$, as in the Droop model, eqn (52) for the growth rate in the DEBf model with $g \to \infty$, $v \to \infty$ and $e = f = 1$, becomes

$$\mu_{m_i,i-1,i} = \frac{v_i}{g_i} \quad \text{and} \quad y_{m_i,i-1,i} = \frac{v_i}{g_i I_{m_i,i-1,i}}. \tag{53}$$

The expression for the yield coefficient is derived using eqn (35) with $f = 1$. This equation can be used

TABLE 2

Parameter set for bacterium-ciliate models, after Cunningham & Nisbet (1983)

Parameter	Units	Value	DEBf model	DEB model
y_{m_1}	–	0·4	$I_{m_1} = 0{\cdot}5 \cdot 0{\cdot}4$	$I_{m_1} = \frac{0{\cdot}5 \cdot 3(l_{d_1} - l_{b_1})}{0{\cdot}4 \ln 2}$
μ_{m_1}	hr^{-1}	0·5	$v_1 = 0{\cdot}5g_1$	$v_1 = \frac{0{\cdot}5g_1 3(l_{d_1} - l_{b_1})}{\ln 2}$
$k_{0,1}$	mg l^{-1}	8		
ρ_1	hr^{-1}	0	$m_1 = 0v_1/g_1$	$m_1 = 0 \frac{v_1 \ln 2}{g_1 3(l_{d_1} - l_{b_1})} = 0$
y_{m_2}	–	0·6	$I_{m_2} = 0{\cdot}2 \cdot 0{\cdot}6$	$I_{m_2} = \frac{0{\cdot}2 \cdot 3(l_{d_2} - l_{b_2})}{0{\cdot}6 \ln 2}$
μ_{m_2}	hr^{-1}	0·2	$v_2 = 0{\cdot}2g_2$	$v_2 = \frac{0{\cdot}2g_2 3(l_{d_2} - l_{b_2})}{\ln 2}$
$k_{1,2}$	mg l^{-1}	9		
ρ_2	hr^{-1}	0·25	$m_2 = 0{\cdot}25v_2/g_2$	$m_2 = 0{\cdot}25 \frac{v_2 \ln 2}{g_2 3(l_{d_2} - l_{b_2})}$

The mass density for both the bacterium and the ciliate is taken equal to 10^{-9} kg mm^{-3}. The cubic root of the volume of the bacterium and ciliate are $l_{d_1} = 0{\cdot}63$ µm and $l_{d_2} = 50{\cdot}4$ µm, respectively. The energy investment ratio for the bacterium is $g_1 = 80$ for the ciliates $g_2 = 1$.

to determine $I_{m_{i-1,i}}$ from $y_{m_{i-1,i}}$ and $\mu_{m_{i-1,i}}$. For the DEB model we take measured values for the length at division l_d. Equation (30) for the growth rate with $g \to \infty$, $v \to \infty$, $e = f = 1$ and $m \to 0$ gives

$$\mu_{m_{i-1,i}} = \frac{v_i \ln 2}{3g_i(l_{d_i} - l_{b_i})} \quad \text{and} \quad y_{m_{i-1,i}} = \frac{v_i}{g_i I_{m_{i-1,i}}}. \tag{54}$$

The equation for the yield is derived using eqn (23). This equation determines the value for the parameter $I_{m_{i-1,i}}$ from given parameter $y_{m_{i-1,i}}$ and the calculated parameter $\mu_{m_{i-1,i}}$ and measured length at division l_d.

Costs for routine metabolism are taken into account as in Nisbet *et al.* (1983). The parameter ρ is expressed as part of the maximum possible specific growth rate μ_m. Finally the saturation constants $k_{i-1,i}$ have the same meaning in all models.

For models with energy reserves we use the body-size scaling relations derived in Kooijman (1986*b*) in order to minimize the number of remaining parameters. For the energy investment ratio g we have $g_2 = l_{d_1}/l_{d_2}g_1$. Hence, when the length at division is supposed to be known, we have two eqns (53) and (53) or (54) for three unknowns, v, g and I. We will give the investment ratio parameter g_1 a specific value and this fixes the values for the other parameters.

In our theoretical study we use the set of parameters proposed by Cunningham & Nisbet (1983) for $\mu_{m_{i-1,i}}$, $y_{m_{i-1,i}}$ and $k_{i-1,i}$ with $i = 1, 2$ (see Table 2). The volumetric length at division for the bacterium is taken equal to $l_{d_1} = 0{\cdot}63$ µm and for the ciliate it is $l_{d_2} = 50{\cdot}4$ µm. For the bacterium we take $\rho_1 = 0$ and $g_1 = 80$ for the ciliate $\rho_2 = 0{\cdot}25$.

For the DM model we get the diagram given in Nisbet *et al.* (1983). The diagram is shown in Fig. 1(a). In the Fig. 1(b) the diagram for the DEBf model with $e = f$ and with energy reserves investment ratios, $g_1 = 80$ and $g_2 = 1$ but without costs for routine metabolism, is shown. The diagram for the Droop model is almost equal to this diagram and is not given separately. From these figures we conclude that the introduction of energy reserves gives washout for much lower dilution rates. This is more apparent for the predator than for the prey because the energy reserves are more important; $g_2 = 1$ whereas $g_1 = 80$.

In Fig. 2 we show the diagram for the DEB model with costs for routine metabolism. Figure 2(a) shows the diagram for the DEB model without energy reserves. The diagram for the Marr–Pirt model is almost equal to this diagram and is not given separately. The results for the DEB model with energy reserves are shown in Fig. 2(b). The diagram for the DEBf model with the same values for the routine metabolism and energy reserves resembles this diagram. Comparison of Figs 1(b) and 2(b) with Figs 1(a) and 2(a), respectively, shows that the introduction of energy reserves in the DM model and in the Marr–Pirt model has the same effect, namely, wash-out for smaller dilution rates and a smaller region of stability. This is clear for there is a hyperbolic relationship of the growth rate with respect to the energy reserves: see eqn (47). The introduction of energy reserves decreases the growth rate, the effect being larger when e is large. This is because e is a density. When an individual grows it has to ingest food which is used partly to maintain the density according the homeostasis. This works as an extra energetic cost for growth and therefore wash-out occurs at lower dilution rates.

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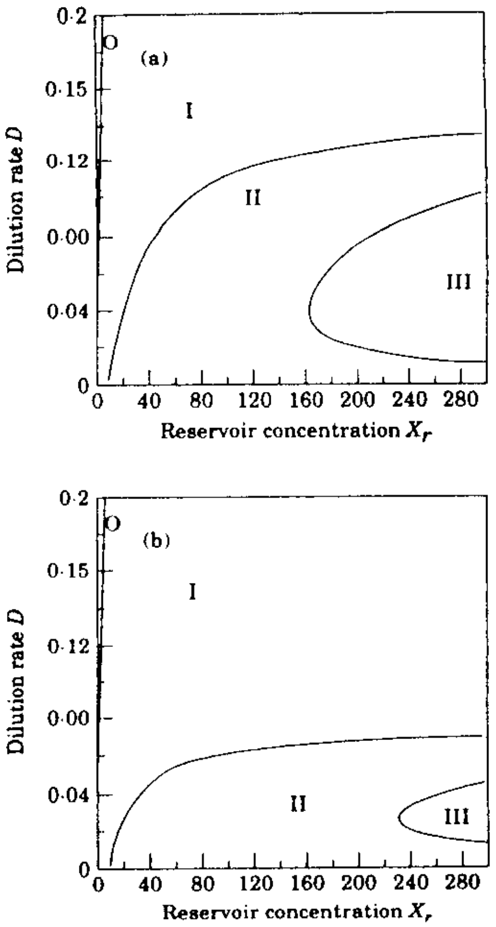

FIG. 2. Operating diagrams for the DEB model with costs for routine metabolism, $\rho_1 = 0{\cdot}0$ and $\rho_2 = 0{\cdot}25$. (a) Diagram for the DEB model without energy reserves. The diagram for the Marr Pirt model resembles this diagram. (b) Diagram for the DEB model with energy reserves, $g_1 = 80$. The diagram for the DEBf model with energy reserves and costs for maintenance resembles this diagram. The values assigned to the physiological parameters are listed in Table 2.

6. Conclusions

Tsangaropoulou & Pavlou (1990) and Sambanis *et al.* (1987) proposed alternatives for the DM model leading to better predictions of these models for experimental data with respect to stability for small dilution rates. In our approach the dynamical population equations are based on realistic mathematical models for individuals making up the populations and result in even better predictions, as shown in the operating diagrams. Nisbet *et al.* (1983) pointed to maintenance to improve correlation. Our results indicate that energy reserves are additionally important.

Droop states that his equation "is an empirical statement and is therefore useful only as long as it fits the facts and is easy to handle". In this paper we showed that his idea fits in the context of a larger theory which leads to a better modelling of food chains in chemostats. In the companion paper (Kooi & Kooijman, 1994) we show that the DEBf model describes the transient behaviour of food chains in remarkable detail. The introduction of energy reserves gives wash-out for smaller dilution rates and a smaller region of stability. The change in shape during growth which leads to surface area being proportional to volume is less important, for the diagrams for the DEBf model and DEB model are almost the same, at least for the chosen parameter values (Kooijman, 1993).

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