



Aggregation Methods in Food Chains

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Abstract—The aim of this paper is to apply aggregation methods to food chains under batch and chemostat conditions. These predator-prey systems are modelled using ODEs, one for each trophic level. Because the models are based on mass conservation laws, they are conservative and this allows perfect aggregation. Furthermore, it is assumed that the ingestion rate of the predator is smaller than that of the prey. On this assumption, approximate aggregation can be performed, yielding further reduction of the dimension of the system. We will study a food chain often found in wastewater treatment plants. This food chain consists of sewage, bacteria, and worms. In order to show the feasibility of the aggregation methods, we will compare simulated results for the reduced and the full model of this food chain under chemostat conditions.

Keywords—Aggregation methods, Food chains, Batch, Chemostat, Logistic equation.

1. INTRODUCTION

Food chains models under batch and chemostat conditions have been studied extensively, we refer to [1,2]. These models generally include a substrate, a prey and a predator, and sometimes even a top-predator. Consequently, the description of the dynamics involves three or more ODEs and many parameters.

In some realistic cases, there are differences in the order of magnitudes of the ingestion and growth rates. An example is a food chain of sewage-bacterium-worms (for example, the water nymph *Nais elinguis*, a oligochaete species) often found in wastewater treatment plants [3–5], there are differences in the order of magnitudes of the ingestion and growth rates. In this paper, we shall take advantage of these different time scales to apply aggregation methods in order to simplify the models for the dynamics of the system.

Perfect aggregation allows to reduce exactly the dimension of a dynamic system. New global variables are defined, which allows one to describe the dynamics of the system in a condensed way [6,7]. In previous papers, we used perturbation techniques to perform approximate aggregation which have been applied to complex ecological models [8]. The method works when the fast system possesses a stable equilibrium [9] and also with a stable limit cycle [10].

In ecological models, it is usually assumed that the lowest trophic level grows logistically. As a consequence, these models do not obey mass conservation laws. In this paper, the lowest level is nonviable and the models for the dynamics of the food chains are derived using the mass conservation law which imposes a constraint on the state variables. This facilitates the reduction

of the system by one variable, that is, by perfect aggregation. The aggregated variable is defined as first integrals of the whole system. Generally, mass conservation laws also provide first integrals which are needed to derive the aggregated system of a lower dimension for an ecological system, where spatial or behavioral heterogeneity are taken into account [8,9]. For the food chains studied here, we assume homogeneous mixed populations. Singular perturbation techniques can be applied for approximate aggregation when ingestion and growth rates are smaller in higher trophic levels. The method resembles the one applied to slow-fast systems in [11–13], for instance, forest pest models. Generally, with a perturbation technique the slow variables are frozen when the equilibria of the fast system are calculated. In our approach, these slow variables are treated as time dependent parameters. This facilitates incorporation of higher-order terms for the slow system. This gives a better approximation without extra computational efforts.

We will consider two environmental conditions for the food chain, namely, the batch and the chemostat. For batch cultures, we start with three ODEs. Because of conservation of mass, one is able to decouple the system into two ODEs and one for the total biomass being the first integral of the system. Because of the different time scales, we can approximate the system further by one ODE for the predator only. We start with linear functional responses and continue with Holling type II functional responses. In the case of linear functional responses, the aggregated system is described by the well known logistic growth equation. The carrying capacity and the intrinsic growth rate are expressed in terms of parameters of the full system, as well as the initial conditions for the state variables. In the case of the chemostat, these results can be obtained only under particular initial conditions. In general, the resulting equation for the growth of the predator is the logistic growth equation with time-varying parameters, the intrinsic growth rate and the carrying capacity.

2. BATCH CONDITIONS

Let $x_0(t)$ and $x_1(t)$ denote the mass density of the resources, respectively, the biomass densities of the prey. A simple model for well-mixed populations without death in a closed region is a set of two coupled ordinary differential equations (ODEs)

$$\frac{dx_0}{dt} = -I_{0,1}x_1 \frac{x_0}{k_{0,1}}, \quad (1)$$

$$\frac{dx_1}{dt} = \mu_{0,1}x_1 \frac{x_0}{k_{0,1}}. \quad (2)$$

For the biological meaning of the parameters, the reader is referred to Table 1.

Table 1. Parameters and state variables for both full and reduced model: t = time, m = biomass, v = volume of the region of interest.

Parameter	Unit	Interpretation
t	t	time
τ	t	fast time variable
x_0	$m \cdot v^{-1}$	resource density
x_i	$m \cdot v^{-1}$	biomass density
x_r	$m \cdot v^{-1}$	substrate concentration in reservoir
D	t^{-1}	dilution rate
$k_{i-1,i}$	$m \cdot v^{-1}$	'saturation' constant
$I_{i-1,i}$	t^{-1}	food uptake rate coefficient
$\mu_{i-1,i}$	t^{-1}	population growth rate coefficient
$y_{i-1,i}$	—	yield
r_i	t^{-1}	intrinsic growth rate
K_i	$m \cdot v^{-1}$	carrying capacity

The first equation shows that the resources diminish at a rate proportional to the biomass densities x_1 , and the scaled density of resources $x_0/k_{0,1}$ with proportionality constant, the ingestion rate $I_{0,1}$. The second equation models how resources are converted into biomass. The specific population growth rate is proportional to the scaled density of resources with proportionality constant $\mu_{0,1}$.

One unit of mass of the resources is converted into $y_{0,1}$ units of biomass of the prey, where $y_{0,1} \leq 1$ is called the yield; which we here take to be constant. The fraction of resources that are not converted to biomass remains in the closed region, for instance as faeces which means that the yield is $y_{0,1} = \mu_{0,1}/I_{0,1}$. The initial conditions at $t = 0$ are $x_0(0)$ and $x_1(0)$, the initial densities of resource and biomass, respectively. They complete the mathematical formulation of the problem.

Since neither resources are supplemented nor biomass is harvested, a weighted sum of resources and biomass must remain constant. We may therefore define a weighted sum by

$$C_2(t) = x_0(t) + \frac{x_1(t)}{y_{0,1}}, \quad (3)$$

such that an equivalent set of ODEs reads

$$\frac{dC_2}{dt} = 0, \quad (4)$$

$$\frac{dx_1}{dt} = \mu_{0,1}x_1 \frac{C_2 - x_1/y_{0,1}}{k_{0,1}}, \quad (5)$$

with an initial condition for C_2 from equation (3). In effect, we have decoupled the system.

The solution of equation (4) is $C_2(t) = C_2(0)$. Substitution into equation (5) directly leads to logistic growth model

$$\frac{dx_1}{dt} = r_1x_1 \left(1 - \frac{x_1}{K_1}\right). \quad (6)$$

The parameters r_1 and K_1 are given by

$$r_1 = \frac{\mu_{0,1}}{k_{0,1}}C_2(0), \quad K_1 = y_{0,1}C_2(0). \quad (7)$$

Hence, the intrinsic growth rates r_1 and the carrying capacities K_1 depend on the initial conditions. This case was analysed in [4]. The stable equilibrium values are $x_0^* = 0$ and $x_1^* = K_1 = y_{0,1}C_2(0)$. The resources are eventually exhausted.

2.1. Introduction of a Predator

We introduce a predator ($i = 2$) feeding on the prey ($i = 1$) with ingestion rate $I_{1,2}$. Thus, a bitrophic food chain consisting of resources x_0 , one prey x_1 and one predator x_2 is considered. The prey-to-predator yield is $y_{1,2}$ and we define $y_{0,2} \stackrel{\text{def}}{=} y_{0,1}y_{1,2}$. The equations become

$$\varepsilon \frac{dx_0}{dt} = -I_{0,1}x_1 \frac{x_0}{k_{0,1}}, \quad (8)$$

$$\varepsilon \frac{dx_1}{dt} = \mu_{0,1}x_1 \frac{x_0}{k_{0,1}} - \varepsilon I_{1,2} \frac{x_1}{k_{1,2}}x_2, \quad (9)$$

$$\varepsilon \frac{dx_2}{dt} = \varepsilon \mu_{1,2} \frac{x_1}{k_{1,2}}x_2, \quad (10)$$

where $\varepsilon = 1$. Below, the parameter ε will be used to separate the time scales of the model. We may again introduce a weighted sum

$$C_3(t) = x_0(t) + \frac{x_1(t)}{y_{0,1}} + \frac{x_2(t)}{y_{0,2}}. \quad (11)$$

We obtain an equivalent of equation (4), namely, $\frac{dC_3}{dt} = 0$, now supplemented with equations (9),(10), where $x_0(t) = C_3(0) - x_1(t)/y_{0,1} - x_2(t)/y_{0,2}$ should be substituted. In [14,15], it was pointed out that the resulting model for the lowest trophic level is not the logistic growth model, as is often assumed in ecological models.

When the interaction between prey and resources is much faster than the interaction between predator and preys, that is, when $\varepsilon \ll 1$, it is possible to use the aggregation method. In biological terms, the predator eats slowly (I small), and therefore, it grows slowly (μ small).

The *fast system* reads, with $\tau = t/\varepsilon$ being the fast time variable,

$$\frac{d\bar{x}_0}{d\tau} = -I_{0,1}\bar{x}_1\frac{\bar{x}_0}{k_{0,1}}, \quad (12)$$

$$\frac{d\bar{x}_1}{d\tau} = \mu_{0,1}\bar{x}_1\frac{\bar{x}_0}{k_{0,1}}. \quad (13)$$

In stable equilibrium, the fast variables are $\bar{x}_0 = 0$ and $\bar{x}_1 = y_{0,1}C_2(0)$. The parameter $C_2(0)$ is, however, not a constant of motion for the full system. Therefore, to obtain the reduced model we must replace it by its expression related to $C_3(0)$ which is the constant of motion for the full system

$$C_2(t) = C_3(0) = \frac{\bar{x}_2(t)}{y_{0,2}}. \quad (14)$$

Equation (10), after substitution of the equilibrium values (\bar{x}_0 and \bar{x}_1), becomes the *slow system*. It reads

$$\frac{d\bar{x}_2}{dt} = r_2\bar{x}_2\left(1 - \frac{\bar{x}_2}{K_2}\right), \quad (15)$$

with

$$r_2 = \frac{y_{0,1}\mu_{1,2}}{k_{1,2}}C_3(0), \quad K_2 = y_{0,2}C_3(0). \quad (16)$$

This is the classical logistic equation again. The intrinsic growth rate r_2 is the growth rate on the prey times the constant of motion for the full system. The carrying capacity K_2 is the yield of the predator on resources times the constant of motion for the full system. Because $C_3(0)$ depends on the initial conditions $\bar{x}_0(0)$, $\bar{x}_1(0)$, and $\bar{x}_2(0)$, the same holds true for the parameters r_2 and K_2 .

The solution $\bar{x}_2(t)$ of equation (15) is used to calculate the fast state variables $\bar{x}_0(t) = 0$, and the biomass density of the prey $\bar{x}_1(t)$ using equation (14) together with $\bar{x}_1(t) = y_{0,1}(C_3(0) - x_2(t)/y_{0,2})$. This completes the solution of the reduced system.

3. CHEMOSTAT CONDITIONS

Under chemostat conditions, we have a continuous influx of resources and an efflux of both resources and individuals of the prey. For a linear (Lotka-Volterra) functional response, the foregoing set of equations is modified to read

$$\frac{dx_0}{dt} = (x_r - x_0)D - I_{0,1}x_1\frac{x_0}{k_{0,1}}, \quad (17)$$

$$\frac{dx_1}{dt} = \mu_{0,1}x_1\frac{x_0}{k_{0,1}} - Dx_1, \quad (18)$$

where D is the dilution rate and x_r is the concentration of the resources in the reservoir. It is easy to show that with

$$H_2(t) = x_0(t) - x_r + \frac{x_1(t)}{y_{0,1}}, \quad (19)$$

we obtain the equivalent set of equations:

$$\frac{dH_2}{dt} = -DH_2, \tag{20}$$

$$\frac{dx_1}{dt} = \mu_{0,1}x_1 \frac{H_2(t) + x_r - x_1/y_{0,1}}{k_{0,1}} - Dx_1. \tag{21}$$

Starting the culture such that $(x_0(0) - x_r) + x_{1,1}(0)/y_{0,1} = 0$, $(H_2(0) = 0)$, the set of equations is equivalent to the extended logistic growth equation

$$\frac{dx_1}{dt} = r_1x_1 \left(1 - \frac{x_1}{K_1}\right) - Dx_1, \tag{22}$$

with r_1 and K_1 given by

$$r_1 = \frac{\mu_{0,1}x_r}{k_{0,1}}, \quad K_1 = x_ry_{0,1}. \tag{23}$$

When $H_2(0) \neq 0$, the logistic equation holds only asymptotically for $t \rightarrow \infty$. Substitution of $H_2 = H_2(0) \exp\{-Dt\}$ in equation (21) gives

$$\frac{dx_1}{dt} = \mu_{0,1}x_1 \frac{H_2(0) \exp\{-Dt\} + x_r - x_1/y_{0,1}}{k_{0,1}} - Dx_1. \tag{24}$$

Hence, the predator does not quite grow logistically for general initial conditions.

3.1. Introduction of a Predator

We introduce a predator into the chemostat equations. A bitrophic food chain consisting of resources, a prey, and a predator is considered

$$\varepsilon \frac{dx_0}{dt} = (x_r - x_0)\varepsilon D - I_{0,1}x_1 \frac{x_0}{k_{0,1}}, \tag{25}$$

$$\varepsilon \frac{dx_1}{dt} = \mu_{0,1}x_1 \frac{x_0}{k_{0,1}} - \varepsilon I_{1,2} \frac{x_1}{k_{1,2}} x_2 - \varepsilon D x_1, \tag{26}$$

$$\varepsilon \frac{dx_2}{dt} = \varepsilon \mu_{1,2} \frac{x_1}{k_{1,2}} x_2 - \varepsilon D x_2. \tag{27}$$

A function $H_3(t)$ is now defined as $H_3(t) = (x_0(t) - x_r) + x_1(t)/y_{0,1} + x_2(t)/y_{0,2}$ where we used $y_{0,2} = y_{0,1}y_{1,2}$. It is easy to show that $\frac{dH_3}{dt} = -DH_3$ holds true, and therefore, we have $H_3 = H_3(0) \exp\{-Dt\}$. Starting with $H_3(0) = 0$, the set of equations is equivalent to equation (26) together with equation (27) where x_0 is given by $x_0(t) = x_r - x_1(t)/y_{0,1} - x_2(t)/y_{0,2}$, $t \geq 0$. This relationship is just the mass conservation law for the whole chemostat system and this facilitates perfect aggregation. Three nonnegative equilibria exist. A single positive equilibrium exists when

$$\frac{x_r}{\varepsilon D} > \frac{\varepsilon k_{0,1}\mu_{1,2} + k_{1,2}I_{0,1}}{\mu_{0,1}\mu_{1,2}}. \tag{28}$$

One of the eigenvalues of Jacobian in this equilibrium equals $-\varepsilon D$. Routh-Hurwitz criteria, see for instance [1], can be used to show that the real parts of the other two eigenvalues of the Jacobian have negative real parts when inequality (28) is satisfied. Therefore, the positive equilibrium is stable.

We will now apply the singular perturbation theory in the case that the prey dynamics feeding on resources is fast and that the predator dynamics feeding on the prey is slow. We start assuming that the initial conditions are such that $H_3(0) = 0$. The fast system is then

$$\frac{d\bar{x}_0}{d\tau} = (x_r - \bar{x}_0)\varepsilon D - I_{0,1}\bar{x}_1 \frac{\bar{x}_0}{k_{0,1}}, \tag{29}$$

$$\frac{d\bar{x}_1}{d\tau} = \mu_{0,1}\bar{x}_1 \frac{x_r - \bar{x}_1/y_{0,1} - \bar{x}_2/y_{0,2}}{k_{0,1}} - \varepsilon I_{1,2} \frac{\bar{x}_1}{k_{1,2}} \bar{x}_2 - \varepsilon D \bar{x}_1, \tag{30}$$

where $\tau = t/\varepsilon$ is the fast time variable again. In these equations, the terms with εD and $\varepsilon I_{1,2}$ are retained and this yields a higher-order approximation. When the ingestion rate $I_{1,2}$ of the predator is small, the dilution rate D has to be small in order to prevent wash-out of the predator. In stable equilibrium of the fast system, the biomass density of the prey \bar{x}_1 is obtained from equation (30)

$$\bar{x}_1 = y_{0,1} \left(x_r - \frac{\bar{x}_2}{y_{0,2}} - \varepsilon \frac{k_{0,1}}{\mu_{0,1}} \left(\frac{\bar{x}_2 I_{1,2}}{k_{1,2}} + D \right) \right), \quad (31)$$

and then for the resources

$$\bar{x}_0 = x_r - \frac{\bar{x}_1}{y_{0,1}} - \frac{\bar{x}_2}{y_{0,2}}. \quad (32)$$

Observe that we did not freeze the slow variable \bar{x}_2 at its initial value, as is usually done in singular perturbation technique, see for instance [11,13].

The value for \bar{x}_1 can now be substituted in equation (27) for the slow dynamics of the predator. This yields

$$\frac{d\bar{x}_2}{dt} = \frac{y_{0,1}\mu_{1,2}}{k_{1,2}} \left(x_r - \frac{\bar{x}_2}{y_{0,2}} - \varepsilon \frac{k_{0,1}(I_{1,2}\bar{x}_2/k_{1,2} + D)}{\mu_{0,1}} \right) \bar{x}_2 - D\bar{x}_2. \quad (33)$$

Substitution in equation (33) gives

$$\frac{d\bar{x}_2}{dt} = r_2 \bar{x}_2 \left(1 - \frac{\bar{x}_2}{K_2} \right) - \varepsilon \frac{\mu_{1,2}y_{0,1}k_{0,1}}{\mu_{0,1}k_{1,2}} \left(\frac{I_{1,2}}{k_{1,2}} \bar{x}_2 + D \right) \bar{x}_2 - D\bar{x}_2, \quad (34)$$

which is once more the classical logistic equation again with

$$r_2 = \frac{\mu_{1,2}x_r y_{0,1}}{k_{1,2}}, \quad K_2 = y_{0,2}x_r. \quad (35)$$

When $H_3(0) \neq 0$, the following logistic growth equation with time-variant parameters holds true:

$$\frac{d\bar{x}_2}{dt} = \frac{y_{0,1}\mu_{1,2}}{k_{1,2}} \left(H_3(0) \exp\{-Dt\} + x_r - \frac{\bar{x}_2}{y_{0,2}} - \varepsilon \frac{k_{0,1}(I_{1,2}\bar{x}_2/k_{1,2} + D)}{\mu_{0,1}} \right) \bar{x}_2 - D\bar{x}_2. \quad (36)$$

This is equation (34) with time-variant parameters

$$r_2(t) = \frac{\mu_{1,2}(H_3(0) \exp\{-Dt\} + x_r)y_{0,1}}{k_{1,2}}, \quad K_2(t) = y_{0,2}(H_3(0) \exp\{-Dt\}x_r). \quad (37)$$

The ODE, equation (36), can be transferred into a linear ODE by substitution of a new variable $1/\bar{x}_2$ and thus be readily solved.

3.2. Hyperbolic Functional Response

For the bitrophic food chain in the chemostat with a Holling-type II functional response for the predator-prey interaction, the governing equation read

$$\varepsilon \frac{dx_0}{dt} = (x_r - x_0)\varepsilon D - I_{0,1}x_1 \frac{x_0}{k_{0,1}}, \quad (38)$$

$$\varepsilon \frac{dx_1}{dt} = \mu_{0,1}x_1 \frac{x_0}{k_{0,1}} - \varepsilon I_{1,2} \frac{x_2}{k_{1,2} + x_1} x_2 - \varepsilon D x_1, \quad (39)$$

$$\varepsilon \frac{dx_2}{dt} = \varepsilon \mu_{1,2} \frac{x_1}{k_{1,2} + x_1} x_2 - \varepsilon D x_2. \quad (40)$$

Perfect aggregation is also possible in this case by the introduction of $H_3(t) = x_0(t) - x_r + x_1(t)/y_{0,1} + x_2(t)/y_{0,2}$, so that $\frac{dH_3}{dt} = -DH_3$. Equilibrium values may be found using the

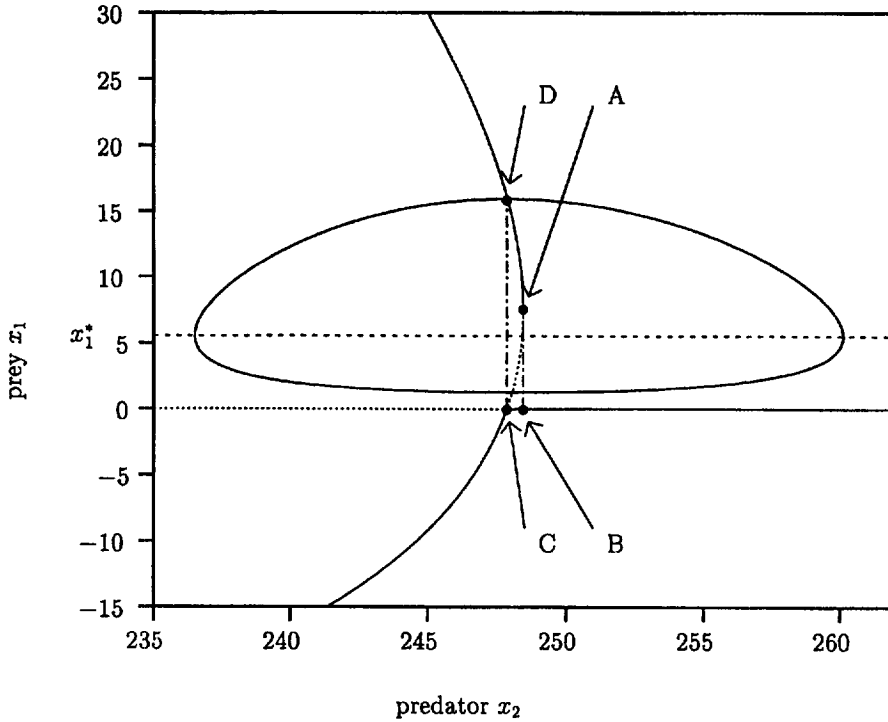


Figure 1. Bifurcation diagram of fast system with $x_r = 1200 \text{ mg dm}^{-3}$. Density of prey as a function of density of predator. Limit cycle is $x_1(t)$ [mg dm^{-3}] as function of $x_2(t)$ [mg dm^{-3}] for full system. The trajectory ABCD is 'limit cycle' for reduced system. Point A is a tangent bifurcation point and point C a transcritical bifurcation point, both for the reduced system. Two stable branches of the fast equilibrium manifolds are $B \rightarrow C$ and $D \rightarrow A$.

procedure described in the previous sections. When the first-order terms are neglected, one equilibrium with $\bar{x}_1 = 0$ is always unstable, while the interior equilibrium point with $\bar{x}_0 = 0$ and

$$\bar{x}_1 = H_3(0) \exp\{-Dt\} + x_r - \frac{\bar{x}_2}{y_{0,2}} \tag{41}$$

is stable. This expression is substituted in the slow system, equation (40),

$$\frac{d\bar{x}_2}{dt} = \frac{\mu_{1,2}\bar{x}_1}{k_{1,2} + \bar{x}_1} \bar{x}_2 - D\bar{x}_2. \tag{42}$$

This result constitutes the reduced system which can be solved numerically. Subsequently, the density of the resources $\bar{x} = 0$ and the density of the prey \bar{x}_1 , equation (41), may be calculated. The slow system, equation (42), has one stable equilibrium. However, it is well known that the full system can possess stable limit cycles. This is associated with the 'paradox of enrichment', that is, for constant D and increasing values of x_r the equilibrium of the full system becomes unstable at a Hopf-bifurcation point. This transition shows that the qualitative behaviours of the two systems differ when higher-order terms are neglected in the aggregation step.

The derivation of the reduced system including higher-order terms proceeds as follows. There are now two fast equilibrium manifolds. One is given by $\bar{x}_1 = 0$. This trivial branch $\bar{x}_1 = 0$ is stable when

$$\bar{x}_2 > \bar{x}_{2TC} = \frac{(\mu_{0,1}(H_3(0) \exp\{-Dt\} + x_r) - \epsilon D k_{0,1})k_{1,2}y_{0,2}}{\mu_{0,1}k_{1,2} + \epsilon I_{1,2}k_{0,1}y_{0,2}}. \tag{43}$$

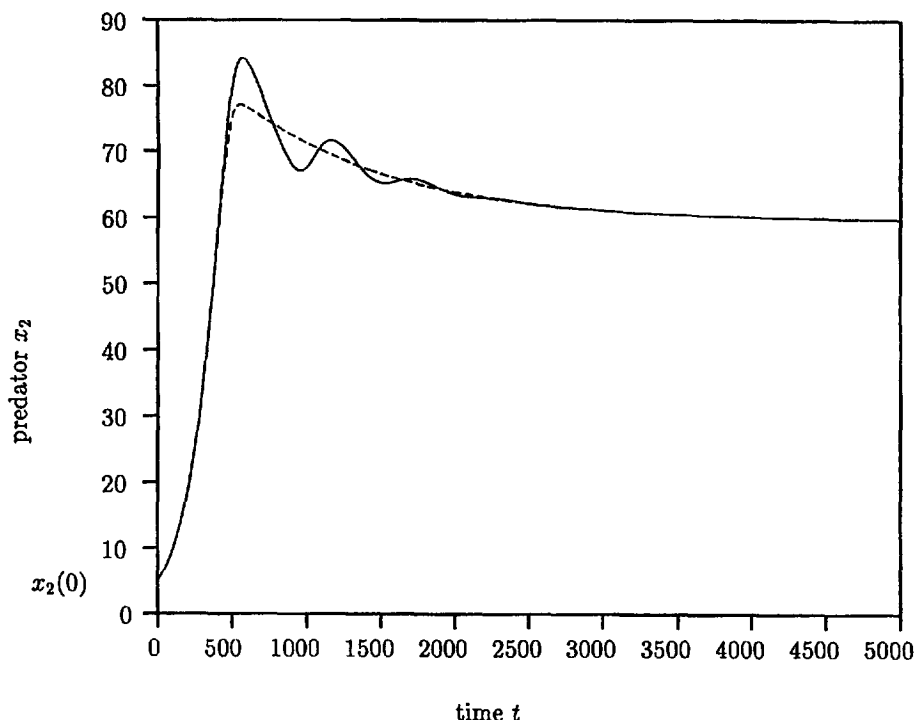


Figure 2. The density of the predator as a function of time t [h], with $x_r = 300 \text{ mg dm}^{-3}$ and initial condition $x_2(t) = 5 \text{ mg dm}^{-3}$. Solid line is for the full system $x_2(t)$ [mg dm^{-3}] and dashed line is for the reduced system $\bar{x}_2(t)$ [mg dm^{-3}].

The other equilibrium manifold is determined by the two roots of the following equation:

$$\begin{aligned} \bar{x}_1^2 - \left(y_{0,1} \left(H_3(0) \exp\{-Dt\} + x_r - \frac{\bar{x}_2}{y_{0,2}} - \frac{k_{1,2}}{y_{0,1}} \right) - \frac{k_{0,1}y_{0,1}}{\mu_{0,1}} \varepsilon D \right) \bar{x}_1 \\ - \left(k_{1,2}y_{0,1} \left(H_3(0) \exp\{-Dt\} + x_r - \frac{\bar{x}_2}{y_{0,2}} \right) - \frac{k_{0,1}y_{0,1}}{\mu_{0,1}} \varepsilon (k_{1,2}D + I_{1,2}\bar{x}_2) \right) = 0. \end{aligned} \quad (44)$$

The point where the discriminant of the quadratic equation (44) is zero constitutes a tangent bifurcation point. The \bar{x}_{1T} value for this point is given by

$$\bar{x}_{1T} = 0.5 \left(y_{0,1} \left(H_3(0) \exp\{-Dt\} + x_r - \frac{\bar{x}_2}{y_{0,2}} - \frac{k_{1,2}}{y_{0,1}} \right) - \frac{k_{0,1}y_{0,1}}{\mu_{0,1}} \varepsilon D \right). \quad (45)$$

When $\bar{x}_{1T} \leq 0$, the nontrivial positive equilibrium manifold is stable. This positive value can be substituted in equation (42) and this yields the reduced system.

In Figure 1, the bifurcation diagram for the fast system is given. When $\bar{x}_{1T} > 0$, there is a tangent bifurcation, denoted by A in Figure 1. For values of $\bar{x}_1 > \bar{x}_{1T}$, the equilibrium manifold is stable whereas for $0 < \bar{x}_1 < \bar{x}_{1T}$, it is unstable. The quadratic equation intersects the $\bar{x}_1 = 0$ axis in a transcritical bifurcation, denoted by C in Figure 1, where $\bar{x}_2 = x_{2TC}$ is given by equation (43). Below the $\bar{x}_1 = 0$ axis, $\bar{x}_2 < x_{2TC}$, the nontrivial branch of the equilibrium manifold is stable again, but here the situation is biologically not relevant. It was shown that in the transcritical bifurcation point, point C in Figure 1, the trivial branch $\bar{x}_1 = 0$ changes also stability.

The trajectory ABCD, which switches between the two equilibrium manifolds, constitutes a quasi-limit cycle for the reduced system. Depending on the initial conditions, the system converges quickly to a stable equilibrium manifold of the fast system. When $\bar{x}_2(0) < x_{2TC}$, it starts on the positive and stable part of the nontrivial branch and when $\bar{x}_2(0) > x_{2T}$, on the stable part of the trivial branch. When $x_{2TC} < \bar{x}_2(0) < x_{2T}$, there are two stable equilibrium manifolds.

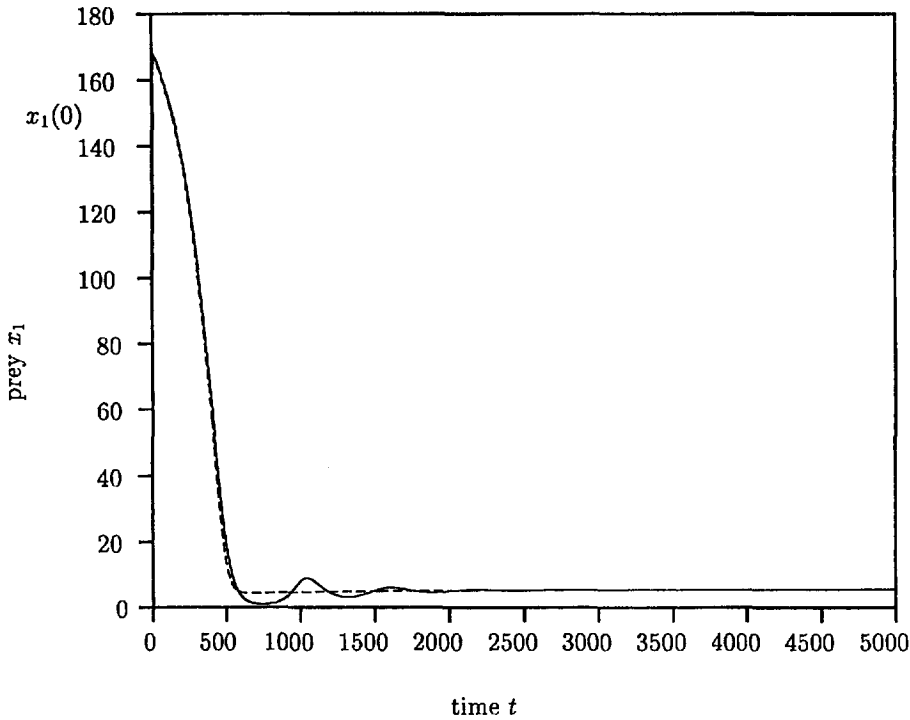


Figure 3. The density of the prey as a function of time t [h], with $x_r = 300 \text{ mg dm}^{-3}$ and initial condition $x_1(t) = 150 \text{ mg dm}^{-3}$. Solid line is for the full system $x_1(t)$ [mg dm^{-3}] and dashed line is for the reduced system $\bar{x}_1(t)$ [mg dm^{-3}].

Table 2. Parameter set for the substrate-bacterium-worms model $I_{i-1,i} = \mu_{i-1,i} / y_{i-1,i}$. Values of control parameters are $D = 0.001 \text{ h}^{-1}$ and $x_r = 300 \text{ mg dm}^{-3}$ or $x_r = 1200 \text{ mg dm}^{-3}$. Initial values of the three state variables are $x_0(0) = 50.0 \text{ mg dm}^{-3}$, $x_1(0) = 150.0 \text{ mg dm}^{-3}$, and $x_2(0) = 5.0 \text{ mg dm}^{-3}$.

Parameter	Units	Values		
		$i = 1$	$i = 2$	
$y_{i-1,i}$	-	0.4	0.6	
$\mu_{i-1,i}$	h^{-1}	0.5	0.01	
$k_{i-1,i}$	mg dm^{-3}	1000	1000	linear functional response
		1000	50	hyperbolic functional response

When $\bar{x}_1(0)$ lies below the curve AC in Figure 1, the system starts on the trivial branch with $\frac{d\bar{x}_2}{dt(0)} < 0$. When $\bar{x}_1(0)$ lies above the curve AC, the system starts on the nontrivial branch with $\frac{d\bar{x}_2}{dt(0)} > 0$. In other words, the curve AC is a separatrix.

As a consequence of the presence of the term $H_3(0) \exp\{-Dt\}$, the fast equilibrium manifolds change slowly in time. For the full system, we have asymptotically $\lim_{t \rightarrow \infty} H_3(0) \exp\{-Dt\} = 0$. The separation criterion [12] applies, that is, when the equilibrium value for the full system satisfies $x_1^* = Dk_{1,2}/(\mu_{1,2} - D) > \bar{x}_{1T}$, the full system has one stable equilibrium. However, when $x_1^* < \bar{x}_{1T}$ the equilibrium is unstable. We conclude that the criterion $Dk_{1,2}/(\mu_{1,2} - D) = \bar{x}_{1T}$, where \bar{x}_{1T} is given in equation (45) with $H_3 = 0$, determines a Hopf bifurcation.

The present bifurcation analysis resembles that of a resources-consumers system analysed in [12], where the renewable resources grow logistically, a Holling-type II functional response is assumed as well as a linear death term for the consumers. That system is equivalent with the system consisting of equations (39) and (40) where $x_0(t) = x_r - x_1(t)/y_{0,1}$, see also [14,15]. With logistic growth of the resources, the relationship equation (44) reduces to a simple parabola, see [12] and it is time-invariant.

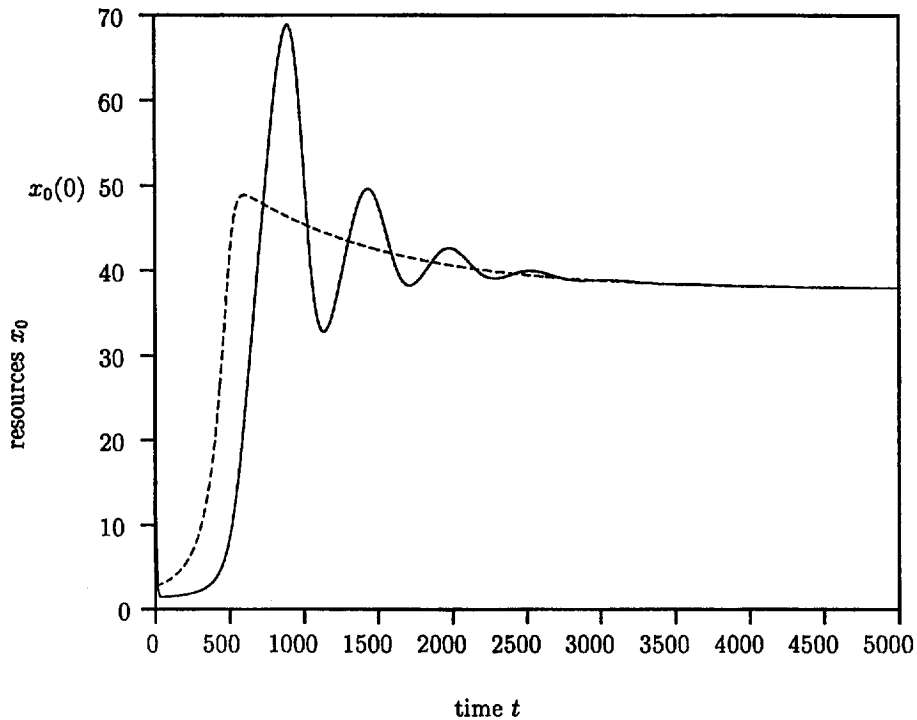


Figure 4. The concentration of the resources as a function of time t [h], with $x_r = 300 \text{ mg dm}^{-3}$ and initial condition $x_0(t) = 50 \text{ mg dm}^{-3}$. Solid line is for the full system $x_0(t)$ [mg dm^{-3}] and dashed line is for the reduced system $\bar{x}_0(t)$ [mg dm^{-3}].

4. SIMULATION RESULTS

For the chemostat system, the solution of the reduced and full systems are compared in Figures 1–4. In Table 2, a survey of the parameter values is given. These values are realistic for a bitrophic food chain consisting of substrate, bacterium, and worm. Such food chains occur in waste-water treatment plants. The values for the bacteria growing on substrate are taken from [16,17], and those for the worms growing on sludge based on data given in [5].

Figure 1 displays for $x_r = 1200 \text{ mg dm}^{-3}$, the calculated stable limit cycle of the full system. We conclude that this limits cycle and that of the reduced system (ABCD) differ considerably. Obviously, the separation of the time scales for the prey-resource and the predator-prey interaction is incomplete for the parameter values used here (Table 2).

When there is a stable equilibrium the situation is more favourable. In Figures 2–4, the time evolution of the three state variables is shown for the full system as well as the reduced system. As is to be expected, the differences for the density of the resources and the prey for small time t are rather large when the initial conditions differ considerably from the equilibrium values. Asymptotically, the predicted biomass densities in the reactor for both models are almost the same. This arises as a consequence of our approach to take higher-order terms (dilution and predation) into account with the calculation of the equilibria of the fast system.

5. DISCUSSION AND CONCLUSION

For a bitrophic food chain application of aggregation methods, perfect as well as approximate, yields a single ODE for the dynamics of the predator. With a linear functional response, this model is the logistic equation in batch condition, whereas in chemostat condition the parameters r and K are generally time varying. When the functional response is hyperbolic the reduced equation is never the logistic equation.

The simulation results show the benefits of the aggregation methods. Time evolution curves for the reduced and full models are rather close to each other after the transient fast process has died out when there is a stable equilibrium of the full system. When the full system has a stable limit cycle, the qualitative behaviour is the same for both the aggregated model and full model, but for the time evolution curves in the limit cycle the difference is not acceptable, given the parameter values used here.

In a forthcoming paper, we will apply the same technique to food webs. In that case there exist several populations at each trophic level. Then the reduced model is not the classical logistic equation but rather the Lotka-Volterra competition model. This means that the resulting dynamics is much richer. For instance, predators at a trophic level can either coexist or exclude each other. It is clear that the applicability of that model for ecological systems, is much broader and also potentially more effective since the reduction of the dimension of the state space can be much larger.

In nature, ecological communities are sometimes composed of groups of species with strong interactions in the same group and weak interactions between different groups corresponding to hierarchically organized communities [18–20]. Numerical simulations of Lotka-Volterra communities involving many species have also shown that after a transient phase during which several populations get extinct, the final structure of the community is hierarchical. In future studies, we intend to use aggregation techniques to simplify hierarchical community graphs. This will be done by aggregating populations of each group into a single compartment described by its total biomass being the aggregated variable. For each isolated cluster, mass conservation laws will be observed.

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