First attempts to model the virus - bacteria interaction in the context of bank filtration

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ABSTRACT

In Berlin the bank filtration plays an important role to obtain drinking water. During the passage of water through the saturated and unsaturated soil zone oxygene, nutrients, pollutants, pathogens etc. pass the system of pores and different kind of interactions take place. Whereas the transport of pathogens coupled with sorption and biodegradation can rather successfully modelled, the biological interaction of bacteriophages with stationary biofilms is still not well understood. Modelling of this kind of interactions is hampered by the poor data availability and by the difficult design of appropriate experiments. Hence only very simple mathematical models with as few parameters as possible may useful for a first qualitative insight. Such a simple model is shown here. As a modelling consequence we cannot exclude that hysteretic effects depending on the direction of water flow may appear.

1. INTRODUCTION

Within the interdisciplinary NASRI research project (Natural and Artificial Systems for Recharge and Infiltration) dealing with bank filtration and artificial groundwater recharge processes, a set of column and field experiments were carried out to understand mechanisms of transport, sorption and biodegradation of different compounds (Nützmann et al. 2004). Parallel to column experiments mathematical simulation models were developed to understand biogeochemical transport processes. The challenge is how to

- handle the complex geochemistry and the
- complexity in sorption processes, due to the potential transport of algae toxins, bacteria and several kind of bacteriophages.

Both modelling efforts are successfully done and are published elsewhere (Holzbecher et al. 2006, Horner et al. 2006). However, a main assumption in the transport modelling work is that the phages do not interact with stationary biofilms or with other microbial species during the transport phase. Furthermore the potential change of sorption behaviour due to interactions of phages with biofilm is not considered yet. Being aware that a modelling of transport, sorption and biological interaction during the passage through soil zones is far too difficult, we began to analyse the interaction of virus with bacteria (serving as hosts in a parasite-host system) and kept the transportation part as simple as possible, as this will be supplied by a more involved simulation model based on the partial differential equation of advection, dispersion and sorption. The aim of this paper is to show the first attempts of virus-biofilm interaction with as simple models as possible.

2. MATERIALS AND METHODS

If bacteriophages can be considered as conservative material during transport processes in the soil zone, then techniques based on partial differential equations, supplied by an equation for sorption and desorption are the appropriate tools for modelling. Well known review papers show how such mathematical models may be constructed and what problems may arise if a closer look is taken to the sorption and filtration behaviour of phages (Massei et al. 2002). In order to keep the things as simple as possible (albeit perhaps oversimplified) a compartment model were selected: The compartment models a single pore, filled with water in which the mobile fraction of bacteriophages interact with bacteria. The bacteria themselves may constitute a) an immobile film (as a stationary phase) or may be b) as mobile as the virus-system. Here we consider only the case a). The compartment is related to an outer system by a simple transport term q*c , where q is the inflow rate of a mobile system and is thought of as related to the pumping rate of a water work.

Virus-bacteria interaction can be considered as a special case of parasite - host interaction system, whereby our basic assumption is that it is sufficient to consider those bacteria or cells which serve as hosts for the bacteriophages and which are at the same time affected by the virus to a certain degree. Parasite - host interactions are often characterized by time delays, which lead (seen on a macroscopic point of view) to an explosive and in general complex temporal behaviour. Hence time retarded differential equations or a time-discrete algebraic equations are often found in the literature. Aiming at a later compatibility with the models, already developed a complete other mathematical structure should be avoided. Therefore finally, we arrive at a modified Lotka-Volterra-model as follows.

$$\frac{dV}{dt} = r_V \cdot B \cdot V^{kr} - m_Z \cdot V^{kv} + q \cdot V_{out} - q \cdot V \qquad (1)$$

$$\frac{d\,B}{d\,t} = r \cdot B \cdot (1 - \frac{B}{cap}) - m_V \cdot B \cdot V^{kb} \qquad (2)$$

The first equation describes the differential mass balance of virus-concentrations (state variable V), whereas the second one that of the bacteria (state variable B). As mentioned above the bacteria are considered as constituting an immobile film. The terms are explained in Table 1. The quantities k_r, k_v and k_b are thought of as parameter, by which time delay and the "outbursting effect" of bacteriophages are approximately modelled, i.e. if V in an term V^x is greater 1 than the effect is enhanced , whereas if $V < 1$ the effect of virus is depressed. In order to avoid a cumbersome notation the parameters k_r, k_b and k_v are called "virus-parameter". Originally it was tried to introduce a C-source for different bacteria. However, due to the complex geochemistry and the poor characterized community of bacteria we decided to introduce a nutritional capacity, cap. The initial values which may play a crucial role in such highly nonlinear systems are not important for this study, as we take our focus on the properties of the stationary system.

TABLE 1 Terms and parameters of Eq. 1 and 2

Term	Explanation	Parameters	Remark
$r_V \cdot B \cdot V^{kr}$	Growth of phages, depending on hosts, B	r_V: specific growth rate kr: (see text)	
$m_Z \cdot V^{kr}$	Mortality of pages	m_Z: specifiv mortality rate kr: (see text)	
$q \cdot V_{out}$	inflow of phages	q: inflow (pumping) rate	This term should be replaced by a more sophisticated approach
$-q \cdot V$	outflow of phages	q: outflow rate Increasing biofilm may change the pore volume and hence the outflow dynamics	This term should be replaced by a more sophisticated approach
$r \cdot B \cdot (1 - \frac{B}{cap})$	logistic growth law	r: specific growth rate for bacteria cap: carrying capacity	We are only considering one type of bacteria. See text.
$- m_V \cdot B \cdot V^{kb}$	mortality of bacteria due to virus-interaction	mV: mortality rate kb: see text	Note that bacteria might be eliminated by other processes than starvation and virus - interaction. This, however is neglected here

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3. RESULTS

3.2 Time-dependencies. Although our main focus is on the analysis of the stationary equation system, we show an example of the oscillating behaviour of the system: Certainly it depends on the values of m_z and m_v whether the amplitudes decline remarkably or not. An example is given in Figure 1, in which the oscillating behaviour and the dependence on k_v is shown. Calculations were performed on the platform MATLAB©.

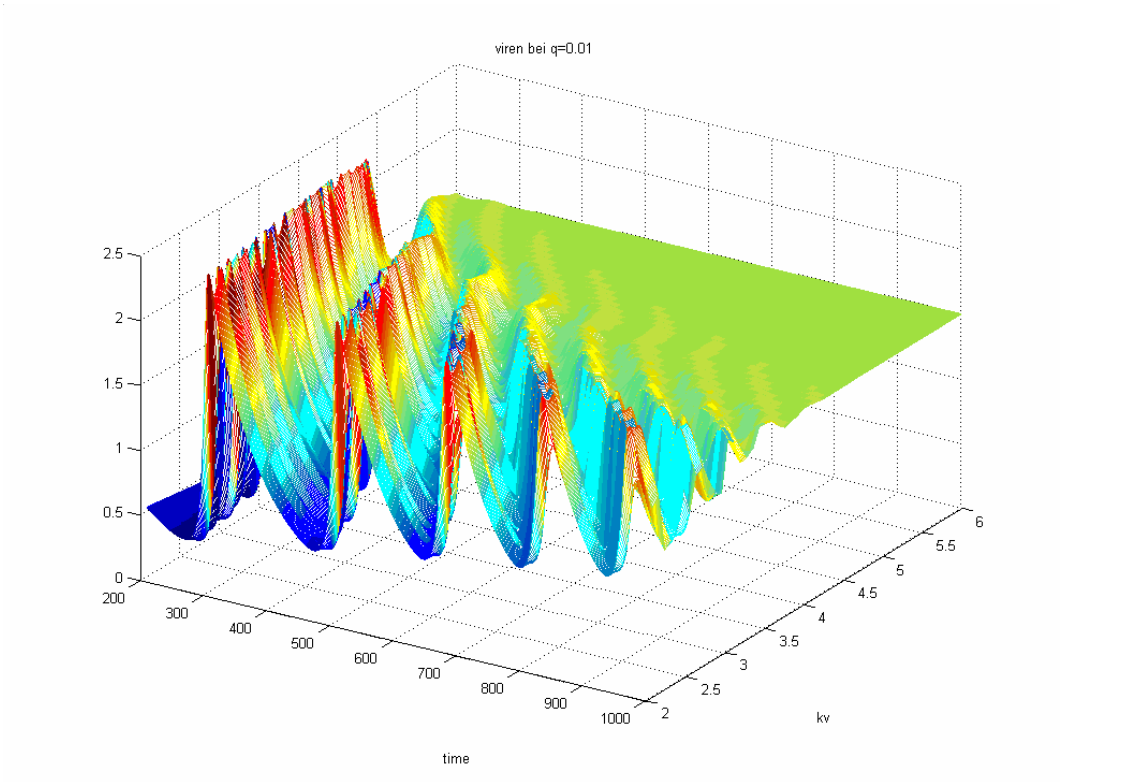

FIGURE 1: Concentration of bacteriophages as a function of time and k_V.

As the time and the parameters are selected arbitrarily it is not meaningful to discuss in detail the time dependency.

3.2 Stationary behaviour. The appropriate tool to analyze the stationary behaviour , especially the dependence of stationary values of the bacteriophages- and bacteria - concentration on parameters of interest, namely

- cap (as substitute for nutrition, i.e. dissolved organic carbon and others) and
- q (as substitute for the pumping rate)

is the concept of zero-isoclines, often applied in ecology .
From the stationarity conditions

$$\frac{dV}{dt}=0 \text{ and } \frac{dB}{dt}=0$$

two nonlinear equations in the state variables V and B evolve, namely
$0=f_1(B,V,\vec{p})$ and $0=f_2(B,V.\vec{p})$.
The symbol $\vec{p}$ encompasses all parameters of the model (1) and (2). There are two algebraic functions f_1 and f_2 and a simultaneous solution, which generally can only be found by numerical methods, provides a set of stationary points $V_{stat}(i)$ and $B_{stat}(i)$ as a function of $\vec{p}$. The index I labels the different possible solutions of the algebraic equation system. In the concept of zero-isoclines the two equations provided by f_1 and by f_2 are solved separately in order to get two sets:

$$B_V := \{(B,V): f_1(B,V,\vec{p})=0 \ \}$$

and

$B_B := \{(B,V): f_2(B,V,\vec{p}) = 0\ \}.$

One may draw a graph B versus V derived from B_V (which we call $B_V(V)$ and another one from B_B ($B_B(V)$) and - obviously - the intersection points are identical with the stationary points, mentioned above. The advantage of the zero isocline concept is, that the two graphs $B_V(V)$ and $B_B(V)$ can be discussed in dependence of parameters, constituting p. Hence if one parameter, for example q is selected a series of graphs $B_V(V, q)$ and $B_B(V, q)$ arises and one can graphically identify how the intersection points vary with q. The same can be done with cap, hence the graphical tool of zero isoclines gives a quick and clear impression about the dependence on the main influencing factors for virus- and bacteria population. Another advantage is that the stability of stationary solutions can be checked by means of graphical techniques, see [….].

3.3 Hysteretic behaviour. The graphs $B_V(V)$ and $B_B(V)$ can be combined and the stability points analyzed. The result is schematically shown in Figure 2:

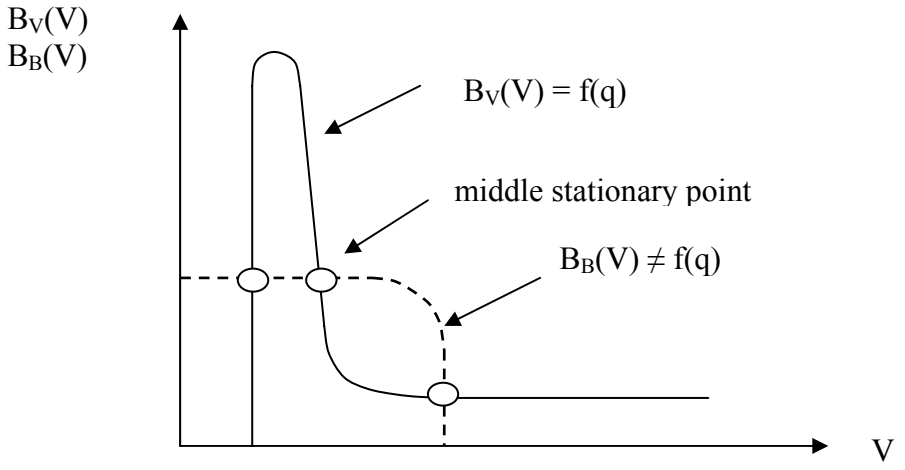

FIGURE 2: Combination of both graphs $B_V(V)$ and $B_B(V)$ in one diagram

The nature of the three stationary points in the standard collection of parameter values (see below) was numerically determined, it turns out that the middle stationary point is unstable, whereas the other two show a complex behaviour, depending on the parameter values, selected. Which of the two not unstable points will be the final stationary state depends from the initial values and then from the parameter constellation. In Figure 3 a 3D-plot is shown where the variation of q, that of V and their influence on $B_B(V)$ and $B_V(V)$ can be seen.

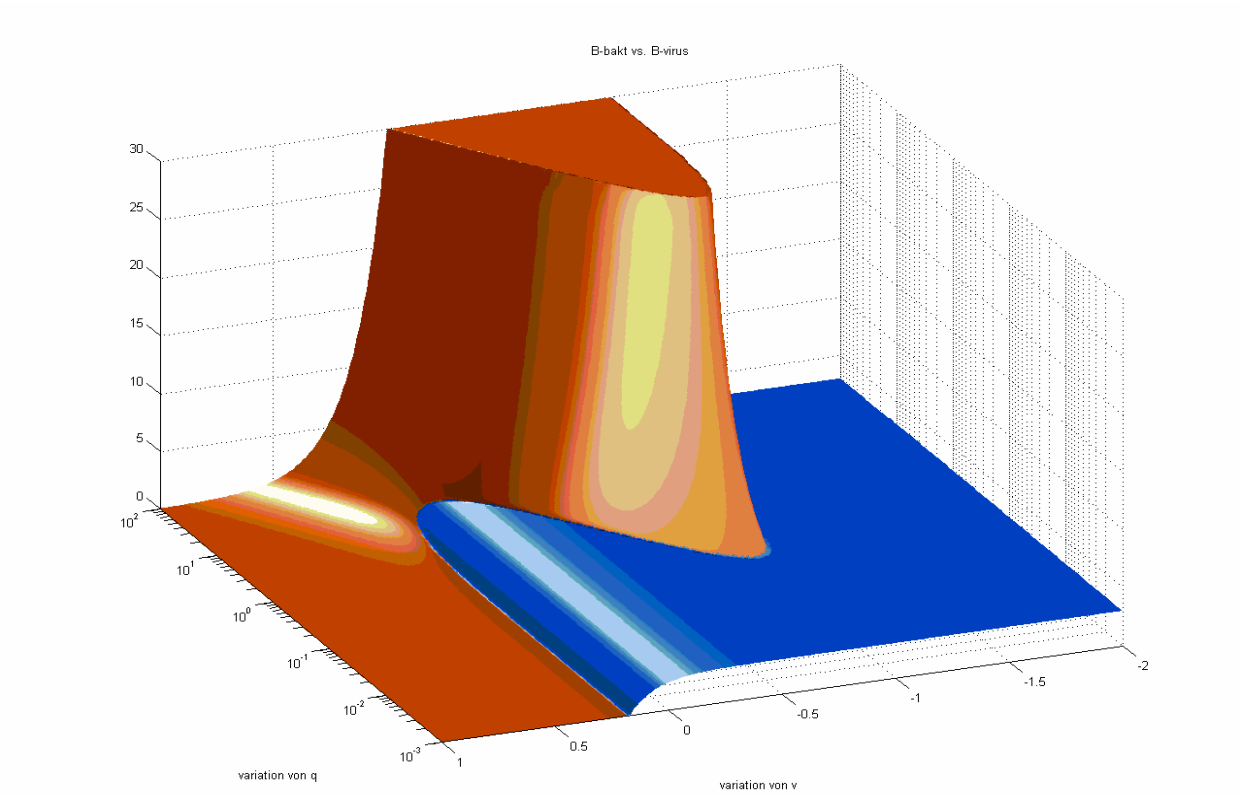

FIGURE 3: Two surfaces are shown which intersect each other. The one independent on q belongs to $B_B(V)$, whereas the other one which depends strongly on q belongs to $B_V(V)$ (V-axis: relative values).

The intersecting line is the set of all stationary points as a function of q and V. As the middle part of the intersection line belongs to unstable points a pumping experiment with increasing q will start with few bacteria and rather high virus concentrations. There is a smooth increase with both, bacteria and virus concentrations until the slope of the intersection line will be vertical. Then a further increasing of the pumping rate will lead to jump where the virus-concentration is on a remarkably lower stationary level whereas that of the bacteria is on a higher level. An increasing of the pumping rate will then get a smooth response by both population. The relationships can be better explained by a projection onto the q, V-plane (Figure 4).

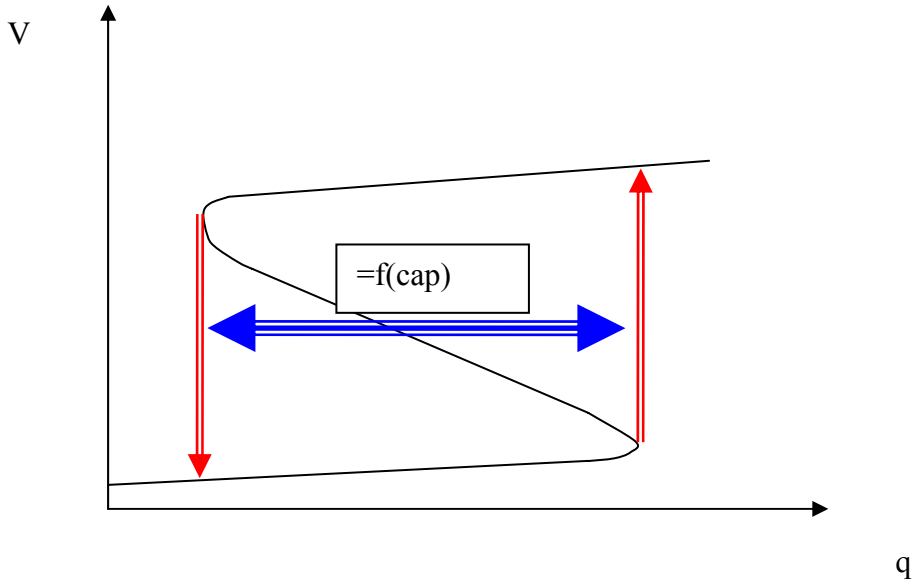

FIGURE 4: Hysteretic behaviour of virus-concentration (and bacteria-concentration, not shown here) as a function of the parameter q.

If the model is approximately correct (including the values of the parameters) then pumping experiments will exhibit a different behaviour: If one starts with low q-values (waiting for stationarity) then the jump to relatively high values appear not until rather high values of the parameter q are selected. If one however starts with high values of q then the jump back to a low level of virus-concentration will be found at rather low values of q.

4. DISCUSSION

There remains many open questions. Many of the parameters could be selected due to the experiences and feeling of the first author. Many other parameters, related more specifically to the virus - behaviour are completely unknown. We performed MATLAB© simulation studies in the way as shown in Figure 3 and concluded that in the main range of all these parameters the oscillating behaviour seems to be the typical one. The virus-parameters k_b, k_v and k_r can have a rather specific influence. However the hysteretic behaviour seem to be modified by actual selected values but not as dramatically as that change we found when we modelled the bacteria as a mobile phase.

Most urgently column experiments are needed where a virus-bacteria system is selected which fits the parasite-host - system. By parameter fitting procedures the high variety of possible parameter values should be more restricted. The main purpose of column experiments however should be to confirm the general assumptions done in deriving the model (i.e. equations (1) and (2)). If the mathematical form will "survive" the following items would be of prior interest:

- Analyzing the parameters how they influence the behaviour of $B_V(V)$ and $B_B(V)$ as function of q (and cap (which was not discussed here).

- Analyzing the systems: (i) both, bacteria and bacteriophages mobile, (ii) virus immobile, bacteria mobile, (iii) virus mobil, virus immobile, bacteria immobile
- Coupling of the biological model to the transport model
- Extending the model to include geochemical reactions

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