

Diauxic Growth and the Ideal Free Distribution

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Introduction

Evolutionary ecology assumes that evolution works, through natural selection, toward a higher individual fitness. Thus, evolution favors those phenotypes that achieve the highest fitness and which cannot be replaced by different phenotypes with the same fitness (these phenotypes correspond to the Evolutionarily Stable Strategies). In the case where organisms can grow on two or more resources they should feed on the resource that provides them with a higher fitness. Fretwell and Lucas (1970) assumed that as the number of individuals feeding on the better resource increases their fitness decreases and, finally, fitness when feeding on the better resource will equal fitness when feeding on the alternative resource. Thus, for yet higher population densities, the consumer population will split over both resources and the animal distribution over the two resources is called the **Ideal Free Distribution**.

The implication of the Ideal Free Distribution for **Population ecology** is that as resources or consumer densities change, the strength with which individuals utilize resources changes too. However, classical population models assume that the interaction strength in food webs is fixed. Thus, the implications of evolutionary ecology are not reflected in these population dynamical models adequately (but see Kompala et al 1986). Recent work (Křivan 1997, Křivan 2003) showed that there is a complex feedback between the IFD and population dynamics of consumers feeding on two resources: the IFD influences population dynamics, which, in turn, define a new species distribution that can be explicitly calculated.

Objectives

Assuming that microbes are evolutionarily optimized, I will study the effects of resource switching on two-substrates-bacteria population dynamics using a model that combines evolutionary optimization with population dynamics. I assume, that bacterial fitness is proportional to the per capita population growth rate. In batch cultures, bacteria, when growing on two resources often utilize these resources sequentially (**diauxic growth**), but simultaneous use of resources was also reported (Egli 1995). In chemostat cultures simultaneous utilization of different substrates typically occurs at low dilution rates while at higher dilution rates bacteria become selective and they utilize only the preferred substrate (Egli 1995).

1. I derive a model which allow us to predict bacterial preferences (i.e., sequential vs. simultaneous substrate utilization) for each combination of resource and bacterial densities. I do that both for **batch** and **chemostat** growth.
2. Using some experimental data I will test, if bacteria switch their resources so that their fitness is maximized

Model

I consider a microbial population with biomass concentration C growing on a mixture of two substrates with concentrations S_1 and S_2 , respectively. The equations governing dynamics of the model are:

$$\begin{aligned} \frac{dS_1}{dt} &= D(S_{01} - S_1) - \frac{1}{Y_1} \frac{S_1}{K_1 + S_1} u C \\ \frac{dS_2}{dt} &= D(S_{02} - S_2) - \frac{1}{Y_2} \frac{S_2}{K_2 + S_2} (1 - u) C \\ \frac{dC}{dt} &= \left(\frac{\mu_1 S_1}{K_1 + S_1} u + \frac{\mu_2 S_2}{K_2 + S_2} (1 - u) - D \right) C \end{aligned} \quad (1)$$

This model is general enough to describe both batch culture as well as chemostat culture. In the chemostat culture the model assumes that substrate levels in the absence of consumers are kept at levels S_{01} and S_{02} , respectively, the uptake of substrates is described by the Monod equation, u is a control variable, and D is the dilution rate. The batch culture is modeled by setting dilution rate $D=0$. Parameters μ_i , K_i , Y_i have the standard meaning. The control parameter u is the preference of microbes for substrate 1. If $u=1$ then all individuals use substrate 1, if $u=0$ then only substrate 2 is used, and values of u between 0 and 1 mean that both substrates are used. The value of control u is not fixed but it changes in time as substrate concentrations change. The question is whether it is possible to predict the time evolution of microbial preference u . I assume, that fitness is proportional to the per capita microbial population growth rate $1/C dC/dt$. This implies that if

$$\frac{\mu_1 S_1}{K_1 + S_1} > \frac{\mu_2 S_2}{K_2 + S_2}$$

then fitness is maximized by utilizing substrate 1 ($u=1$), while if the opposite inequality holds than fitness is maximized by utilizing the other substrate. Consumers that will mimic this strategy most closely will have a higher growth rates than those with different strategies and should therefore spread in the population. Evolution should therefore favor those microbes which follow the above described strategy. Here I assume that $\mu_1 > \mu_2$, i.e. the first substrate is the preferred substrate when it is at high concentrations. Consumer preferences for resources is not uniquely defined along the "switching" curve

$$\frac{\mu_1 S_1}{K_1 + S_1} = \frac{\mu_2 S_2}{K_2 + S_2} \quad (2)$$

Along this curve bacteria achieve the same fitness regardless of the combination of substrates they use. This case corresponds to the Ideal Free Distribution and we show below that population dynamics (1) allow us to compute this distribution exactly.

Batch Culture

Firstly I consider the case of a batch culture which corresponds to setting the dilution rate in model (1) equal to zero ($D=0$). Figure 1 (left column in both panels) shows substrate 1 (solid line), substrate 2 (dashed line), and bacteria (dot line) population dynamics. Parameters and experimental points are those given in Kompala et al (1986). As the concentration of the preferred substrate (glucose) decreases, fitness of bacteria that feed on this substrate decreases too. The corresponding trajectory of model (1) necessarily hits the switching curve (2) and, at this moment, fitness when feeding on substrate 1 will be the same as fitness when feeding on substrate 2. Hitting the switching curve causes the sharp corner in the curve that describes substrate 1 dynamics (Figure 1). From then on the model predicts that bacteria should use both substrates (i.e., either the population becomes polymorphic in which case some bacteria will feed on substrate 1 and others on substrate 2, or the population is monomorphic in which case a single bacteria will use both resources). The control u is such that the substrate concentrations follow the switching curve and the ratio at which the two substrates are utilized (the IFD) is given by

$$\frac{u}{1-u} = \frac{Y_1(S_1\mu_1 - (K_1 + S_1)\mu_2)^2}{K_1 K_2 Y_2 \mu_2^2}$$

Preference u for substrate 1 is shown in Figure 1 (the right column in both panels). We observe that as substrates are depleted the preference for substrate 1 tends to some positive value which depends on the particular combination of the two sugars.

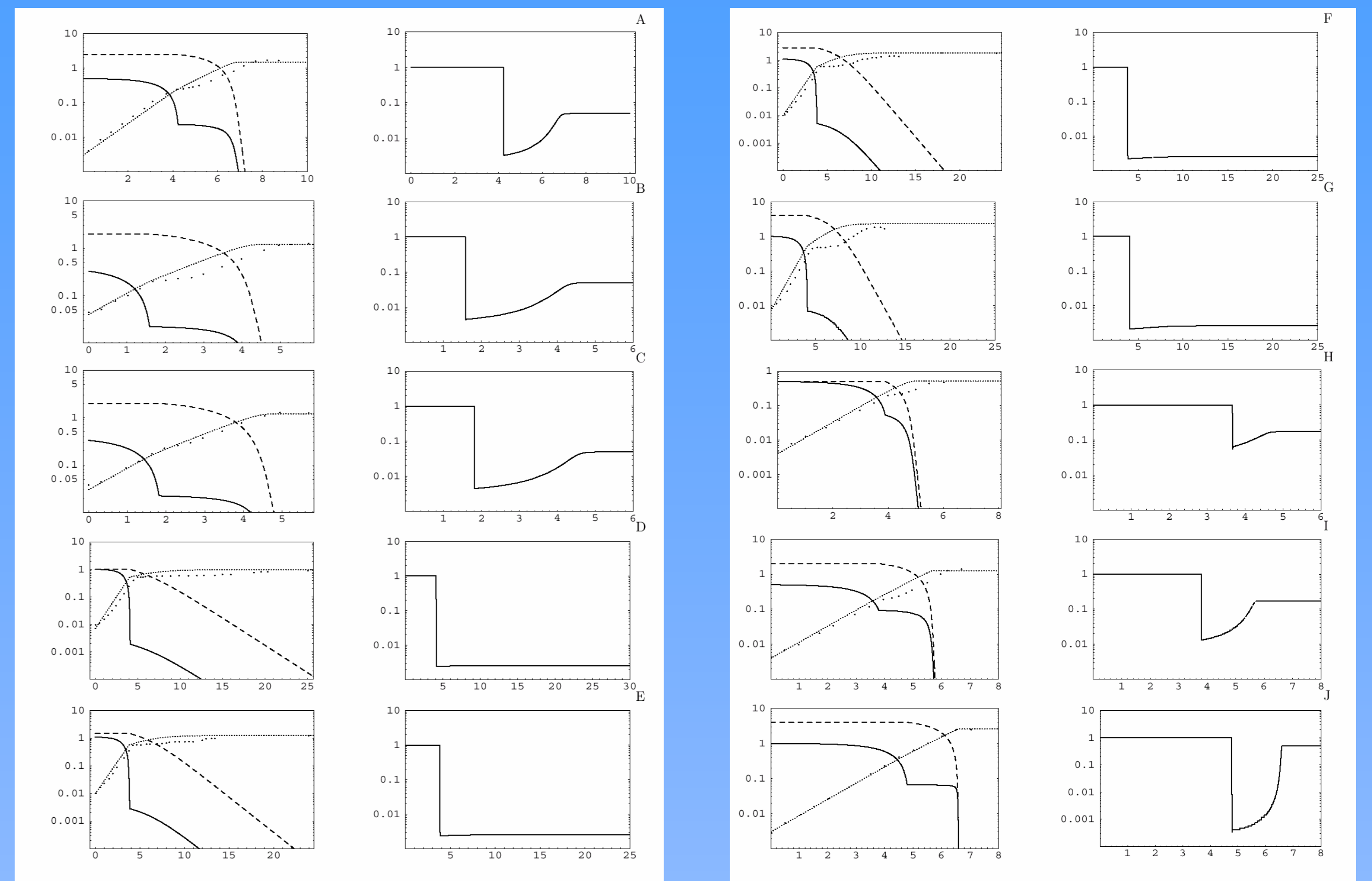


Figure 1: The growth of *Klebsiella oxytoca* on two substrates (data taken from Kompala et al. 1986). The lines are simulations of model (1) for batch growth. The preferred resource (solid line), the alternative resource (dashed line) and *K. oxytoca* (dot line) are shown in the left column of both panels. The right column shows estimated preference of *K. oxytoca* for the preferred resource (glucose).

Substrates	Panel in Figure 1	Observed time of switching [hours]	Predicted time of switching [hours]
glucose-xylose	A	4.2	4.2
glucose-xylose	B	1.7	1.6
glucose-xylose	C	2	1.8
glucose-lactose	D	5	4.1
glucose-lactose	E	4.2	3.8
glucose-lactose	F	4.2	3.8
glucose-lactose	G	4.6	4.2
glucose-arabinose	H	4	3.7
glucose-arabinose	I	4	3.8
glucose-fructose	J	NA	4.8

Table 1: Predicted time [by model (1)] when bacteria should switch from utilizing the preferred substrate only to utilizing both substrates. Observed time of switching was taken from Kompala et al. (1986).

Chemostat

Secondly, I consider the case of chemostat culture where dilution rate D is positive. Again, I assume that bacteria utilize substrates so that their fitness maximizes. The results are shown graphically in Figure 2 where the left panel shows dependence of the equilibria of model (1) on dilution rate D . The right panel shows the corresponding preference for substrate 1 at the population equilibrium. The figure for the case where bacteria are adaptive is qualitatively similar to experimentally obtained profiles (Egli et al. 1993).

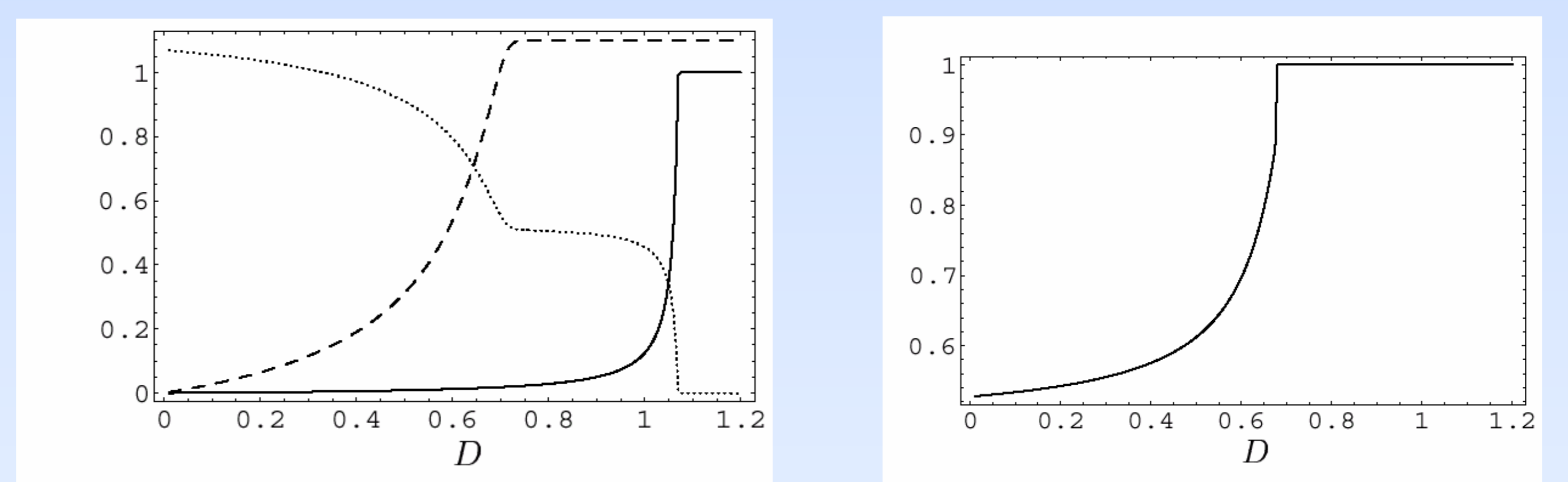


Figure 2: The left panel shows dependence of equilibria (substrate 1-solid line, substrate 2-dashed line, bacteria-dot line) of model on dilution rate D when bacteria behave adaptively. The right panels show the corresponding preference for substrate 1.

Conclusions

1. For batch growth, bacteria should use first the resource that provides them with a higher per capita population growth rate. However, as concentration of this resource decreases, the alternative resource will be also used. Thus, at low concentration of the preferred substrate both substrates will be used simultaneously (Figure 1).
2. Using experimental data I showed that the predicted times when bacteria should switch from feeding on the preferred substrate to feeding on both substrates agree with observations (Table 1).
3. For continuous cultivation the dependence of equilibrium species densities on the dilution rate when bacteria behave adaptively is, qualitatively, in agreement with experimental observations (Figure 2).

References

- Egli, T. 1995. The ecological and physiological significance of the growth of heterotrophic microorganisms with mixtures of substrates. *Advances in microbial ecology* 14:305-386.
- Egli, T., U. Lendenmann, and M. Snozzi. 1993. Kinetics of microbial growth with mixtures of carbon sources. *Antonie van Leeuwenhoek* 63:289-298.
- Fretwell, D.S., Lucas, H.L. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16-32
- Kompala, D. S., D. Ramkrishna, N. B. Jansen, and G. T. Tsao. 1986. Investigation of bacterial growth on mixed substrates: experimental evaluation of cybernetic models. *Biotechnology and Bioengineering* 28:1044-1055.
- Křivan, V. 1997. Dynamic ideal free distribution: Effects of optimal patch choice on predator-prey dynamics. *American Naturalist* 149:164-178
- Křivan, V. 2003. Ideal free distributions when resources undergo population dynamics. *Theoretical Population Biology* 64:25-38.